University of Alberta

REGULATION OF RECRUITMENT IN FATHEAD MINNOWS (*PIMEPHALES PROMELAS*): MULTI-STAGE EFFECTS AND CONSEQUENCES OF SIZE VARIATION

by

RENA ELISABETH VANDENBOS

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science

in

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R Vandenbos

Box 580
Lytton, B. C.
V0K 1Z0

Aug. 29/96

University of Alberta

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **"Regulation of recruitment in fathead minnows (*Pimephales promelas*): multi-stage effects and consequences of size variation."** submitted by **Rena Elisabeth Vandenbos** in partial fulfillment of the requirements for the degree of **Master of Science in Environmental Biology and Ecology**.

Dr. William M. Tonn

Dr. Jens Roland

Dr. Robert Hudson

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ABSTRACT

The processes that underlie the regulation of population size are poorly understood, although density-dependent mechanisms acting within and between different life-history stages, and mechanisms associated with selective survival during early life-history ,are both suggested to be important in controlling recruitment. To test these predictions, I examined how density-dependent mechanisms acting on the adult, egg, larval and young-of-the-year stages of fathead minnows (*Pimephales promelas*) affected the number and characteristics of young-of-the-year fish at the end of their first season; in a related experiment, I examined how differences in mid-season size variation affected size-selective survival of young-of-the-year fathead minnows. Processes acting in both of these experiments affected overall survival, as well as selectivity of survival. Thus, I conclude that these density-dependent mechanisms play an important role in the regulation of recruitment in fathead minnows.

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CHAPTER 1

GENERAL INTRODUCTION

Understanding the regulation of population size remains one of the major unanswered questions in ecology, despite the fact that studies on this subject date back more than sixty years (e.g., Nicholson 1933). In particular, the mechanisms that underlie regulation are poorly understood, although there is consensus that regulation must act through density-dependent processes, such that at low densities population size tends to increase, and at high densities population size tends to decrease (Sinclair 1989; Turchin 1995). Recently, it has been suggested that to fully understand the processes that control recruitment we must explicitly consider differences between individuals; an individual's characteristics, relative to others in the population, may strongly influence its chance of survival (Huston et al. 1988; Crowder et al. 1992; VanWinkle et al. 1993). Despite this conceptual progress, our understanding of how density-dependent mechanisms act within and between different life-history stages is poor (Sinclair 1989; Turchin 1995), especially in species with stage structured life histories such as fish, amphibians, and insects (Sinclair 1989). Also, despite the recent advances gained through the individual-based approach, we still do not fully understand how variation among individuals may affect how many, and which, individuals survive.

Because different life stages do not exist in isolation of each other in most natural situations, understanding how density-dependent mechanisms act and interact during each stage is essential for a full understanding of how these mechanisms control population size. Density-dependent processes acting within and between different life-stages are

especially understudied in fishes (Sinclair 1989), yet throughout their lives, as their body size increases by several orders of magnitude, fish are typically exposed to many processes that can determine how many individuals recruit to the adult population. The density of the adult population may control not only egg production (Wootton 1990), but also mortality of eggs and young-of-the-year (YOY) fish via cannibalism (Polis 1981; Smith and Reay 1991); competition between older and younger cohorts may also be important (Hamrin and Persson 1986). Yet many studies on YOY recruitment tend to focus on only the larval or YOY stage (Miller et al. 1988; Fox and Flowers 1990; Pepin 1993), and interactions with adults are rarely examined. On the other hand, studies that focus on other stages, such as the egg stage, are often linked to mechanisms involving adults, but these studies tend to be behavioural in focus and do not examine the consequences of egg-adult interactions on YOY recruitment (Whoriskey and Fitzgerald 1985; Brodeur et al. 1991; Cote and Gross 1993). Therefore, we need to resolve how density-dependent mechanisms may be acting within particular stages, and especially how they interact between different life-history stages, before we can hope to understand what controls population size in fish.

Another area that has been understudied, yet may be important in determining population abundance, is the amount of variation within and among YOY cohorts in characteristics such as growth rate, age, and size. It has been suggested that the probability of survival can vary substantially among members of a cohort due to differences in these characteristics (Post and Prankevicius 1987; Miller et al. 1988; Crowder et al. 1992). Recent studies demonstrate that differences in the amount of

variation in these characteristics during the first season of life can affect both overall survival and the characteristics of the survivors, yet these studies have either been model- (e.g., Crowder et al. 1992; Rice et al. 1993) or laboratory-based (e.g., Ellis et al. 1993; Folkvord and Ottera 1993). Studies of fish populations in more natural settings are needed to determine if mechanisms linked to variation in characteristics are actually important in determining which individuals survive, as well as how many survive.

Because density-dependent factors acting within, or between, life stages may control the amount of variation in characteristics such as age, size, growth rate and hatch date, they may thus indirectly control recruitment into the adult population through mechanisms other than direct density-dependent mortality. For example, the length of the breeding season (variation in hatch dates) may be affected by density-dependent growth in adult fish, as populations with smaller adults often have more protracted breeding seasons (Danylchuk and Fox 1994). In turn, variation in hatch dates directly affects variation in both the age and size-distributions of YOY, which can then affect overall survival of the YOY and their recruitment into the adult population. Density-dependent competition within and between life-stages may also lead to high variation in size and growth rate of cohorts, since competition can promote unequal food intake among competitors (Rubenstein 1981; Lomnicki 1988). Because density-dependent mechanisms acting within and between different life-history stages have strong potential to control recruitment, and because variation in characteristics in early life-stages may play a role in determining how many, and which, individuals survive, it is essential to understand the ramifications of

mechanisms linked with both if we wish to understand what controls population size in fish.

To address some of these issues I ran several different experiments in ponds, enclosures, and the laboratory. To determine how density-dependent mechanisms may operate within, and interact between, different life-stages I stocked different densities of fathead minnows (*Pimephales promelas*), a small bodied fish species common throughout North America, into experimental ponds; processes acting on these fish, on the eggs they produced, and on the resulting offspring during the first season of life were quantified (Chapter 2). I performed another set of experiments in enclosures set within another pond to determine if variation in size distributions of YOY cohorts is important in determining the rate and selectivity of survival (Chapter 3). Finally, I ran a set of laboratory experiments to determine how vulnerable YOY fish were to cannibalism by different adult size-classes (Chapter 3). Together, I hoped that these experiments would illustrate whether or not processes acting both within and between life stages had measurable effects on recruitment of YOY in more realistic settings than have been used in previous studies. In Chapter 4 (General discussion), I assess how the results of these experiments, and my approach, met my original objectives.

LITERATURE CITED

Brodeur, R. D., K. M. Bailey, and S. Kim. 1991. Cannibalism on eggs by walleye pollock *Theragra chalcogramma* in Shelikof Strait, Gulf of Alaska. Marine Ecology Progress Series 71: 207-218.

Cote, I. M., and M. R. Gross. 1993. Reduced disease in offspring: a benefit of coloniality in sunfish. Behavioral Ecology and Sociobiology 33: 269-274.

Crowder, L. B., J. A. Rice, T. J. Miller, and E. A. Marschall. 1992. Empirical and theoretical approaches to size-based interactions and recruitment variability in fishes. Pages 237-255 *in* D. L. DeAngelis and L. J. Gross, editors. Individual-based approaches in ecology: concepts and individual models. Chapman and Hall, New York, New York, USA.

Danylchuk, A. J., and M. G. Fox. 1994. Seasonal reproductive patterns of pumpkinseed (*Lepomis gibbosus*) populations with varying body size characteristics. Canadian Journal of Fisheries and Aquatic Sciences. 51: 490-500.

Ellis, S. C., W. O. Watanabe, and W. D. Head. 1993. Effect of initial age variation on production of Florida red tilapia fry under intensive, brackishwater tank culture. Aquaculture and Fisheries Management 24: 465-471.

Folkvord, A., and H. Ottera. 1993. Effects of initial size distribution, day length, and feeding frequency on growth, survival, and cannibalism in juvenile Atlantic cod (*Gadus morhua* L.). Aquaculture 114: 243-260.

Fox, M. G., and D. D. Flowers. 1990. Effect of fish density on growth, survival, and food consumption by juvenile walleyes in rearing ponds. Transactions of the American Fisheries Society 119: 112-121.

Hamrin, S. F., and L. Persson. 1986. Asymmetrical competition between age classes as a factor causing population oscillations in an obligate planktivorous fish species. Oikos 47: 223-232.

Huston, M. A., D. L. DeAngelis, and W. M. Post. 1988. New computer models unify ecological theory. BioScience 38: 682-691.

Lomnicki, A. 1988. Population ecology of individuals. Princeton University Press, Princeton, New Jersey, USA.

Miller, T. J., L. B. Crowder, J. A. Rice, and E. A. Marschall. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. Canadian Journal of Fisheries and Aquatic Sciences 45: 1657-1670.

Nicholson, A. J. 1933. The balance of animal populations. Journal of Animal Ecology 2: 132-178.

Pepin, P. 1993. An appraisal of the size-dependent mortality hypothesis for larval fish: comparison of a multispecies study with an empirical review. Canadian Journal of Fisheries and Aquatic Sciences 50: 2166-2174.

Polis, G. A. 1981. The evolution and dynamics of intraspecific predation. Annual Review of Ecology and Systematics 12: 225-251.

Post, J. R., and A. B. Prankevicius. 1987. Size-selective mortality in young-of-the-year yellow perch (*Perca flavescens*): evidence from otolith microstructure. Canadian Journal of Fisheries and Aquatic Sciences 44: 1840-1847.

Rice, J. A., T. J. Miller, K. A. Rose, L. B. Crowder, E. A. Marschall, A. S. Trebitz, and D. L. DeAngelis. 1993. Growth rate variation and larval survival: inferences from an individual-based size-dependent predation model. Canadian Journal of Fisheries and Aquatic Sciences 50: 133-142.

Rubenstein, D. I. 1981. Individual variation and competition in the Everglades pygmy sunfish. Journal of Animal Ecology 50: 337-350.

Sinclair, A. R. E. 1989. Population regulation in animals. Pages 197-241 *in* J. M. Cherrett, editor. Ecological concepts. Blackwell Scientific Publishers, Oxford, UK.

Smith, C., and P. Reay. 1991. Cannibalism in teleost fish. Reviews in Fish Biology and Fisheries 1: 41-64.

Turchin, P. 1995. Population regulation: old arguments and a new synthesis. Pages 19-37 *in* N. Cappuccino and P. W. Price, editors. Population dynamics: new approaches and synthesis. Academic Press Inc., New York, NewYork, USA.

VanWinkle, W., K. A. Rose, and R. C. Chambers. 1993. Individual-based approach to fish population dynamics: an overview. Transactions of the American Fisheries Society 122: 397-403.

Whoriskey, F. G., and G. J. FitzGerald. 1985. Sex, cannibalism and sticklebacks. Behavioural Ecology and Sociobiology 18: 15-18.

Wootton, R. J. 1990. Ecology of teleost fishes. Chapman & Hall, London, UK.

CHAPTER 2

REGULATION OF RECRUITMENT OF YOUNG-OF-THE-YEAR FATHEAD MINNOWS (*PIMEPHALES PROMELAS*): CASCADING LIFE-HISTORY INTERACTIONS AND THE ROLE OF DENSITY-DEPENDENCE

INTRODUCTION

Following Nicholson's (1933) introduction of the concept of population regulation via density-dependent factors, and the subsequent decades of debate (e.g., Andrewartha and Birch 1954; Den Boer 1968), there is now a general consensus that the regulation of animal populations, when it occurs, operates through density-dependent mechanisms (Sinclair 1989; Godfray and Hassell 1992). Nevertheless, recent reviews suggest that for almost every group of animals, we still have a poor understanding of where density-dependence occurs in the life-cycle, how frequently density-dependent mechanisms operate in different life-stages, and how these various mechanisms interact (Sinclair 1989; Turchin 1995).

For many organisms it is commonly thought that the regulation of population size has its roots in processes acting during the early life history; because this life-stage typically comprises the largest number of individuals, small changes in survival rates can lead to large differences in terms of final number of survivors (Miller et al. 1988; Arcese et al. 1992). However, despite its importance, regulation of the recruitment of young into adult populations remains one of the least understood phenomena in ecology. Initial attention focused on the numerical relationship between adult population size (or "stock")

and the number of eggs or offspring ("recruits") they produce (Ricker 1954; Beverton and Holt 1957). Recently, researchers have taken a more mechanistic approach (Hopper et al. 1996; Maret and Collins 1996), concentrating on processes occurring during the early life-history stage, but as a consequence of this approach, these studies are often conducted in isolation of other stages.

For fishes, processes occurring during the young-of-the-year (YOY) stage are thought to be important in determining population abundance (Ricker 1975; Cushing 1981; Crowder et al 1992), and these have been the focus of numerous recent studies. Survival of fish during their first growing season may be selective with respect to hatch date (Rice et al. 1987; Schultz 1993; Cargnelli and Gross 1996), growth rate (Post and Prankevicius 1987; Hovenkamp 1992; Rice et al. 1993), and body size (Post and Prankevicius 1987; Miller et al. 1988; Margulies 1990; Litvak and Leggett 1992); large body size in YOY fish also improves survival during the first winter (Post and Evans 1989; Shuter and Post 1990; Johnson and Evans 1996).

The amount of variation in characteristics such as growth rates, ages, and sizes both within and among cohorts may also affect the intensity and selectivity of survival in YOY fishes (Crowder et al. 1992; Rice et al. 1993) and other taxa (Maret and Collins 1996), and many of these characteristics may be affected by intra-cohort densities. However, most studies in natural systems only estimate, often rather roughly, initial YOY density, as adequate sampling of YOY fish is difficult, especially in the earliest stages. In addition, although inter-cohort processes are clearly important in the dynamics of YOY fish, many studies have been done on YOY in isolation of other life stages (Fox and

Flowers 1990; Miller et al. 1988; Pepin 1993). Information on adult density is sometimes incorporated (Post and Prankevicius 1987; Elliot 1989) but mechanisms associated with adult density are rarely examined; the few studies that do so involve taxa other than fish (Harris 1987), are theoretical in nature (DeAngelis et al. 1991; Barlow 1992), or are actually more focused on mechanisms occurring within the adult stage (Tonn et al. 1994).

In most natural situatuations, however, different life stages do not exist in isolation of each other. By limiting studies to mechanisms occurring within only one or two life-history stages, potential mechanisms, and interactions among mechanisms, that can have important consequences on population size, may be missed. For instance, YOY recruitment may be influenced both directly and indirectly by adult density, via cannibalism by adults (Polis 1981; Dominey and Blumer 1984; Smith and Reay 1991) and competition between older and younger cohorts (Hamrin and Persson 1986; Harris 1987; Hill 1992). As well, the initial conditions (e.g, initial density, timing of hatch, distribution of sizes among the cohort) that YOY experience may determine which individuals survive, yet to fully understand these initial conditions, we must also understand how processes acting on eggs operate and how they are influenced by adult populations.

Although studies on YOY fish tend to be conducted in isolation of other life stages, mechanisms occurring during the egg stage are often linked to mechanisms affecting adults. Egg production may be affected by density-dependent growth during the adult stage since fecundity is often related to adult body size (Wootton 1990). Egg survival may also be directly related to adult density. Adults in high density populations may be less able to defend their eggs against predators, due to their smaller size or poorer

condition (Mappes and Kaitala 1994). As well, cannibalism of eggs by adults is a frequent occurrence in fishes (Smith and Reay 1991), and would be expected to be density dependent (reviewed by Polis 1981; see also Hyatt and Ringler 1989; Brodeur et al. 1991; Valdez-Szeinfeld and Cochrane 1992).

However, although studies of mechanisms occurring during the egg stage in fish populations often incorporate interactions with other life stages, these studies tend to have more of a behavioural focus. Thus, they do not directly examine the consequences of these interactions to YOY recruitment, although the regulatory potential of mechanisms acting during the egg stage is often suggested. In addition, quantification of eggs is extremely difficult in most field settings, with the consequence being that egg production or survival is usually only roughly estimated (similar to larval fish). In addition, most studies concentrate on either production (Fox 1994) or survival of eggs (e.g., Brodeur et al. 1991; Valdez-Szeinfeld and Cochrane 1992), but not both.

Until the occurrence, strength and especially the interactions of density-dependent mechanisms are better understood, we can not hope to fully understand what controls population size in fish. In particular, we need to resolve how mechanisms acting during the larval and older stages may interact, and to determine if (and how) mechanisms acting on the egg stage play a role in the regulation of population size. To facilitate these studies, we need to find a system where all the pertinent life history stages can be easily quantified.

In an attempt to resolve some of these issues I stocked different densities of fathead minnows (*Pimephales promelas*) into experimental ponds; processes acting on

these fish, on the eggs that they produced, and on the resulting offspring during their first season of life were quantified. The experiment was run in two different summers for one full growing season in each year; some information on overwinter survival was also collected. My objectives were to determine: 1) if young-of-the-year survival through the first growing season was influenced (directly or indirectly) by density-dependent processes acting on adults; 2) if and how egg stage dynamics could play a significant role in controlling recruitment; and 3) whether a consideration of the density-dependent mechanisms acting and interacting during different life-stages enhances our understanding of population regulation.

METHODS

Natural history

The fathead minnow (*Pimephales promelas*) is a small-bodied cyprinid fish widely distributed in North America. In the boreal region of Alberta, which is the northwestern limit of its range (Scott and Crossman 1973), fatheads are common in small lakes and ponds lacking piscivores; they frequently coexist with other small-bodied species but also occur in single-species assemblages (Robinson and Tonn 1989). Fatheads are omnivorous, eating a combination of algae, detritus and small invertebrates (Price et al. 1991). Three summers are typically required for these fish to reach maturity in Alberta, compared with one or two summers at lower latitudes (Held and Peterka 1974). Males establish small nesting territories and, following spawning, guard a nest of eggs laid on the

underside of structures such as plants or logs (McMillan and Smith 1974). Eggs take only 5 d to hatch at 25° C but the duration of incubation is temperature-dependent (McMillan and Smith 1974). Adults are fractional spawners, so they can spawn more than once in a breeding season (Gale and Buynak 1982), but there is high post-reproductive mortality, especially among males (Markus 1934).

Because of these life history traits, fathead minnows are easy to sample, observe, and use in experimental settings. Fathead minnows reproduce readily in small ponds when provided with nesting substrates. Because of the habit of establishing and guarding nests on the underside of structures, including artificial structures, the eggs are easy to find and enumerate. This habit of laying on artificial substrates also permits manipulation of the type of sites available for nesting territories. Eggs show definite developmental stages, visible to the unaided eye, which assist in tracking the fate of egg batches. Finally, all age-classes, including eggs, are easy to sample using traps, electrofishing, seining and examination of nest sites (personal observation).

In north-central Alberta, fathead minnow populations are frequently subject to winterkill, but the populations rebound quickly (personal observation), suggesting strong mechanisms operate that allow rapid recovery and persistence.

Experiment

This study was conducted at the University of Alberta's Meanook Biological Research Station, located in north-central Alberta (54° 37′ N, 113° 35′ W). The experiment was run for a full growing season in each of two years, from spring (late May) to near ice-up (late September).

Two research ponds (360 m^2 surface area and 1.3 m deep) were divided in half by a polyvinyl curtain. The bottom of this water-impermeable curtain was attached to a metal sleeve, which was buried into the substrate on the bottom and sides of the pond. The curtain was supported by 2.5 m wooden stakes so that it extended well above the water level. Abundant nesting substrate (ten floating 1.8 m fenceboards tied to weights) was provided for the adults. Prior to stocking fathead minnows, the ponds were raked and any other structures suitable for nesting were removed so that I could quantify total egg production by checking the nest boards.

I manipulated the initial densities of fish by adding equal numbers of mature males, females and immature juveniles (collected from nearby natural ponds) to each of the four pond halves at two density levels: 1 and 4 fish/ m^2. There were two replicates of each treatment in each year, systematically assigned in an alternating fashion to the four pond halves. The densities used represent average (1 fish/ m^2) and high end (4 fish/ m^2) densities seen in a nearby natural, unmanipulated population (W. Tonn, personal communication). In a preliminary experiment these treatments resulted in differences in growth but not survival of stocked fish.

Males (≥70 mm total length (TL)) and females (≥ 63 mm TL) were identified by secondary sexual characteristics, tubercles on males and ovipositors on females. Juveniles (two size-classes: 40-49 mm and 50-56 mm TL) were defined as smaller fish that had no visible secondary sexual characteristics. Fish were marked with either a fluorescent elastomer injection (1994; Northwest Marine Technology Inc., Shaw Island, WA) or fin clipping (1995) to differentiate the groups throughout the experiment.

Data collection

I monitored stocked populations to determine if the density treatments were maintained (i.e., mortality rates similar) and if the two densities resulted in differences in growth rates and condition. Stocked populations were sampled monthly by setting five Gee minnow traps overnight in each pond half; this level of sampling caught 90% of the stocked fish the day after stocking (unpublished data). Captured fish were counted, examined for marks, sexed, measured (TL) and returned to the ponds. During the September 1994 sampling captured fish were also weighed to determine condition ($(mass/TL^3)*100$).

Throughout the spawning season, I examined nest boards daily to measure the production and fate of eggs. Thus, for every egg batch, its date of appearance was recorded, its location mapped, and the number, stage of development and state (alive, depredated, diseased) of all eggs were estimated. Based on previous observations, I assigned eggs into three developmental stages (see also Nagel 1976). Newly laid eggs were fairly opaque, containing primarily yolk, and no eye development in the embryo could be discerned. In the second stage, eyes were visible to the unaided eye; under the microscope, eggs at this stage were about half full of yolk. In the final stage, eggs were strikingly gold-tinted and hatched quickly (usually within 48 hours). This final egg stage corresponded to eggs that had little or no yolk, and had embryos with retinal development, which was responsible for the gold tint.

To quantify egg production, I identified any egg batches with eggs in the first stage of development where there had not been any eggs the previous day. The numbers of

eggs in these batches were estimated daily by counting up to 200 eggs in the center of the batch, determining the area that this number of eggs occupied, and then extrapolating from the area of the entire batch to obtain the total number of eggs in the batch. Any eggs laid in a dispersed manner were counted individually. Therefore I was able to keep track of individual batches and could quantify the total number of eggs laid in each pond half every day.

I monitored the fate of the egg batches from the time they were laid to the time they disappeared. The number of diseased eggs (determined by the presence of fungal hyphae) seen in any batch was recorded. Egg batches that disappeared before the third stage of development could not have hatched and were recorded as depredated (crusts of partially eaten eggs were inevitably observed in these cases). Eggs that disappeared after reaching the third developmental stage were recorded as hatching successfully (there were no egg crusts left behind after hatching).

To determine mid-season size distributions of YOY fish in each pond half and to monitor their densities, I sampled the successfully hatched YOY fish in five 2.5-m net hauls (0.4 m diameter, 1 mm mesh) on July 14, 1995 (one month after hatching began). All YOY fish caught were preserved in 95% ethanol. A similar sample taken in 1994, but preserved by freezing, was lost when the freezer broke.

In the fall, ponds were drained to about 30 cm depth and as many fish as possible were removed. Adults were removed by three day continuous sets of minnow traps (previous to draining) and by seining. YOY fish were removed with seine hauls. Ponds were seined until two hauls in a row produced less than five fish. All fish removed were

preserved in 95% ethanol. These fish were later counted, weighed and measured (TL) to determine recruitment rates, final sizes, and final conditions of YOY fish. Pond temperature at removal was about 4° C in 1994 and 9° C in 1995. Ice-up occurred within two weeks of removal of fish in both years.

In the spring of 1995 a small number of fish remained in the ponds (which were no longer divided as the curtains were removed in the fall after draining). These fish were removed by electrofishing about 10 d after the ice melted and measured (TL) to compare the fall and spring final size distributions and determine if overwinter survival was size-selective.

Analysis

Because treatments were paired within ponds, all analyses were paired to control for pond effects. Paired t-tests were used for comparisons of average or total measures (egg production, number of eggs hatched, proportion of eggs surviving, YOY final abundance, YOY fish survival, YOY final mean size, average condition ((mass/length^3)*100)). All size distributions were compared using the Kolmogorov-Smirnov two-sample test.

Because curtains had been removed after draining occurred in the fall, the overwintered fish caught in the spring of 1995 contained fish from both treatments. I therefore compared their percent frequency size distribution with that of all fish in the fall (regardless of pond or treatment) to assess if overwinter mortality was selective.

In 1995, one of the two ponds flooded in mid-August, shortly after the mid-season sampling of YOY. Therefore I had four replicates of each treatment for egg production

and survival but only three replicates for data collected after the reproductive season and mid-season net hauls (i.e., YOY survival, final lengths, mass, condition).

All statistical analyses used are outlined in Sokal and Rohlf (1981). Analyses were performed using Systat (version 5.0 for Windows; Wilkinson 1992).

RESULTS

Stocked fish

Density differences between treatments were maintained throughout the experiment in both years. Although there were the expected declines in catch rates following post-spawning mortality, there were always at least three times as many stocked fish in the high adult density treatments (HDA) as in the low adult density treatments (LDA) during the monthly trapping samples (Fig. 2-1).

There were too few mature males and females (marked size-classes) remaining at the end of the season to make any meaningful comparisons of growth. The two juvenile (age-1) size-classes grew consistently better in the LDA treatment than in the HDA treatments (Fig. 2-2). There were no significant differences in stocked fish condition ((mass/length^3)*100) at the end of the season in 1994 (paired t-test, t=2.758, df=1, P=0.22),

Egg production and hatching success

Males were observed guarding territories on nest boards within two days of stocking in both years. The first egg batches appeared within one week in 1994 and

within two days in 1995. The number of egg batches being guarded at any one time peaked during the first two weeks of the reproductive season, yet there were always empty nest sites available. Surprisingly, empty nest sites were especially common in the HDA treatments, where there were usually less than three or four egg batches present at any one time after the first week. The maximum number of egg batches observed on one board was thirteen, but five or six batches on a board was more usual. Egg batches began disappearing within three days of laying each year. In HDA treatments, schools of stocked fish were observed mobbing guarding males and chasing males off their territories. Afterwards, I always observed the signs of egg predation, where partially eaten eggs, crusts, and other debris were all that was left of previously recorded egg batches.

The number of eggs produced in any given pond half ranged from 13,000 to 38,000 (Fig. 2-3.A). The results suggested an effect of pond, especially in 1994, as well as of treatment. There were fewer eggs found in HDA treatments (paired t-test, $t=3.286$, $df=3$, $P=0.05$), but the difference was fairly small, ranging between 6% to 26%. Since egg predation was so much higher in the HDA treatments (see below), it may be that this result does not reflect a real difference in production; rather it could have been the result of my sampling only once a day, between which batches could be produced and eaten but never recorded. There were several occasions where I witnessed crusts of eggs in a location where there had been no batch the day before, and I can only assume that eggs were also added to older batches and consumed before I observed them.

Despite the similar number of eggs produced in both treatments, there were dramatic differences in the number of eggs surviving to hatch (Fig. 2-3.B.). Significantly

fewer eggs hatched in the HDA than in the LDA treatments (paired t-test, t=3.765, df=3, P=0.033). Survival of eggs was significantly higher in the LDA treatments; averaging 76% in LDA treatments but only 18% in HDA treatments (paired t-test on arcsine square root transformed proportions, t=5.864, df=3, P=0.01).

The primary cause of egg loss was predation; only 1-5% became diseased. Diseased eggs were obviously white or showed evidence of fungal hyphae and lingered for many days before disappearing, whereas most losses were sudden disappearances of entire batches, with only crusts of eggs left behind as described above. Most of this predation was actually cannibalism by other stocked fish. There were no other vertebrate predators in the ponds, and trapping revealed no obvious differences in potential invertebrate predators, e.g. dytiscid beetles and odonate larvae (personal observation). Because of cannibalism, therefore, high adult density populations had low survival of eggs, leading to significantly fewer eggs hatching compared with those pond halves with low adult densities.

Young-of-the-year production and survival

Net hauls on July 12, 1995 yielded dramatic differences in YOY fish between treatments. Not surprisingly, given the number of eggs that hatched, there were many more YOY in the LDA treatments. However, there was an intracohort density effect on YOY growth, as YOY were larger in the HDA treatments than in the LDA treatments (Pond one: HDA $\bar{x}$=19.2 mm, LDA $\bar{x}$ =15.3mm; Pond two: HDA $\bar{x}$=17.5mm, LDA $\bar{x}$=12.4mm). Overall, the size distributions were significantly different (Kolmogorov-

Smirnov two sample test, Pond three: max. diff.=0.629, P=0.001, Pond four: Max diff.=0.68, P<0.001; Fig. 2-4).

Although HDA pond halves had low initial densities of YOY and LDA pond halves had high initial densities of YOY, numbers of YOY in the fall (when ponds were drained) showed much less variability in comparison with initial YOY densities; five of the six pond halves had 1,850-5,000 YOY regardless of treatment (Fig. 2-5). As a result, there were no treatment effects on the number of YOY at the end of the season (paired t-test, t=0.691, df=2, P=0.561). The exception was the LDA treatment in pond four (1995), which had very low survival (200 YOY). Interestingly this pond half had the highest initial number of fry (Fig. 2-3.B).

Since there were such large treatment related differences in initial number of YOY in the ponds, yet little difference at the end of the season, it was not surprising that survival was strongly related to treatment (Fig. 2-6). The proportion of YOY surviving the season was significantly higher in the HDA treatment than in the LDA treatment (paired t-test on arcsine square root transformed proportions, t=7.139, df=2, P=0.019).

Although there were large treatment effects on YOY production (number of eggs hatched), there was also considerable variability within, as well as between, treatments. As a result, there was a large range in the actual number of YOY produced among all of the ponds (Fig. 2-3.B). HDA pond halves initially produced 2,400-11,000 YOY whereas 10,600 to 30,500 YOY were produced in the LDA replicates, resulting in an overall thirteen-fold range in initial number of YOY. Similarly, considerable variation in the proportion of YOY that survived the summer (Fig. 2-6) could not be explained by the

treatment. Because density of YOY fish has been demonstrated to affect mortality rates of fish during their first year (e.g., Myers and Cadigan 1993; McMenemy 1995), I re-analyzed mortality of YOY using initial number of YOY as a covariate, with adult density as the treatment effect. Initial number of YOY actually explained the majority of the variability in mortality among both sets of treatment populations and, in fact, relegated stocked fish density to a marginally non-significant role (Fig. 2-7, Table 2-1). A straight linear regression (ignoring treatment) of mortality as a function of initial number of YOY described 93% of the variation in mortality (Fig. 2-7).

Because mortality in YOY is often selective with respect to various characters, characteristics of survivors at the end of the season may differ among populations having different mortality rates (which, in this experiment, also corresponded to both the ≥ age-1 fish density and initial YOY density). However, there was no effect of treatment on the mean size of the YOY that survived the first season (paired t-test, t=0.298, df=2, P=0.794, Fig. 2-8). Nor was there an effect of treatment on coefficient of variation of the final size distributions (paired t-test, t=2.44, df=2, P=0.135, Fig. 2-9). Coefficient of variation was, however, consistently lower in all LDA treatments than in HDA treatments. Although the condition index of YOY fish at the end of the season appeared to be higher in the HDA treatments, especially in ponds one and four (these were the pond halves with the highest overall survival, see Fig. 2-6), the difference was not significant (paired t-test, t=2.232, df=2, P=0.15, Fig. 2-10).

I also regressed these characteristics (mean size, condition, and coefficient of variation of the final size distribution) against both initial number of YOY and mortality.

Mortality was analyzed as the logit of mortality (or the log of the odds of dying = #dead/ final#alive) as this measure represents the actual magnitude of differences in mortality, rather than just proportion dying. As with the analyses comparing treatments (adult densities), there were no significant relationships between mean size and either initial number of YOY or mortality (Table 2-2). Likewise, there was no linear relationship between condition and either initial number of YOY or mortality (Table 2-2). In contrast, the coefficient of variation of the final YOY size distribution of a given population was strongly related to both initial number of YOY (Fig. 2-11.A) and mortality (Fig. 2-11.B, Table 2-2). Final size distributions were less variable in cohorts with high initial densities and high mortality.

Overwinter survival (Sept. 1994 - May 1995)

A small number of YOY were not removed during the seining in the fall. About 10 days after the ice melted in the following spring (water temperatures were 5°C), ponds were again drained and all remaining fish were removed by electroshocking. The size distribution of these fish differed significantly from the size distribution of fish before ice-up (Kolmogorov-Smirnov two sample test; $P<0.001$). Just before ice-up, most individuals were small (12-20mm), whereas most individuals that survived the winter were larger than 30mm (Fig. 2-12).

DISCUSSION

Understanding the processes underlying the regulation of population size is one of the oldest (Nicholson 1933) but most pressing problems facing ecologists. It seems clear

that regulation occurs through density-dependent mechanisms, but these mechanisms are still poorly understood (Sinclair 1989). This is especially true for taxa with stage-structured life histories e.g., fish and insects (Sinclair 1989; Myers and Cadigan 1993), where we know little about when these mechanisms operate, how strong they are, and how these density-dependent mechanisms interact between different life-stages (Harris 1987).

Although it is generally thought that processes acting during the early life-history are of critical importance to the regulation of fish populations, there are actually many life-stages during the first season of life for a fish, e.g., eggs, larvae, YOY fish, and any or all may potentially interact with each other and with older cohorts in the population. Because density-dependent mechanisms can act differently at different life-history stages in fish populations, it should be rewarding to better understand how density affects the different stages, and how processes may interact among stages to control population size.

As a generalization, density-dependent mortality is common in early-life stages of fish whereas growth and reproduction, rather than mortality, are more often functions of density during the adult stage (Charnov 1986); this was the case in my experiment also. However, survival of eggs depended on the density of adults and, in turn, YOY growth and mortality was directly dependent on the resultant intracohort densities. My experiment thus illustrates that interactions within and between life stages do have a strong ability to affect abundance and characteristics of YOY fish at the end of their first season of life, and this indicates that a focus on only a single stage (e.g., larvae) can restrict our understanding.

Because mortality of stocked fish was independent of density, the treatment differences of stocked fish density were maintained throughout the experiment. Density was not without its effects on the stocked fish, however; mirroring results observed by Tonn et al. (1994) in a whole pond experiment with crucian carp, growth of the smaller size-classes of stocked fish was density-dependent. The mechanism underlying the growth reduction was most likely related to exploitation competition, as Tonn et al. (1994) could demonstrate, but may also have been due, in part, to density-related differences in the activity level of fish (Fox and Flowers 1990). In either case, these results indicated that the two densities that I used, based on levels observed in a natural population in different years, were different enough to have biologically meaningful effects on the adult population.

The treatment (stocked fish density) may also have interacted directly or indirectly with other stages to affect the recruitment of YOY fish. Egg production was significantly but not strongly related to adult density; rather, there was a stronger pond effect. Although egg production is frequently positively related to body size and condition (Wootton 1990), there were no initial differences in adult size or condition in my experiment. Because adults began reproducing within a week of being stocked, it is not surprising that the number of eggs produced was not strongly related to adult density. Differences in growth of stocked fish may have contributed to any differences in egg production that occurred later in the season. However, it is more likely that the lower egg production measured in high density treatments was an artefact of the daily sampling regime; in the treatments with high egg cannibalism (HDA), it was more likely that an egg

batch was laid and eaten before I could record it. The pond effect suggests that there may have been some factor other than the density of spawners regulating egg laying; one factor that did not limit egg production was the availability of nesting sites. There were always empty nest sites available, especially in the high density treatment.

Nevertheless, there was a strong interaction between adults and eggs, as eggs were eaten in a strongly density-dependent manner by the adults. The sheer numbers of conspecifics in high density ponds likely overwhelmed guarding males, gaining access to nests (Hyatt and Ringler 1989). Indeed, on several occasions I witnessed schools of fish mobbing nest-guarding males in high density treatments and noted that nests were cannibalized completely in each case. Raiding is probably more successful when there are more individuals in a school (Whoriskey and FitzGerald 1985). As well, reductions in the guarding male's condition, due to the increased activity required to defend nests and continually restart the nesting process, could limit his ability to defend nests (Unger 1983), and males were clearly defending their nests much more actively in the high density treatments (personal observation). Finally, because food was likely more limiting in the HDA treatment, as indicated by the lower growth of stocked fish, eggs likely became a preferred food item (Polis 1981).

Following the hatching of eggs, direct interactions between larvae and YOY fish with other life stages, especially adults, appeared to be of less importance than effects of intracohort interactions. Although competition with adults may occur (e.g., Harris 1987), and cannibalism rates may be higher on larvae at high densities of adults (Polis 1981), YOY survival was actually higher in the HDA treatments than in LDA treatments in my

experiment. Had I not quantified the processes affecting egg mortality, it would have appeared that adults actually increased survival of YOY fish (inverse density-dependence). Instead, this apparent positive relation between adults and YOY resulted from a "cascading" life-history interaction (sensu Carpenter et al. 1985), i.e. an indirect effect of the negative interaction between adults and eggs. Survival of YOY fish was density-dependent, but not (directly) on densities of adult fish; rather densities within their cohort (intracohort) appeared critical. Indeed, there was an almost perfect relationship between mortality of YOY fish and initial number of larval fish (Fig. 2-7), overpowering any relationship with stocked fish density. The apparent relationship between adult density and YOY survival was thus superficial. These results clearly illustrate the need to determine not only what mechanisms act during different life-history stages, but how they may interact, to correctly understand population regulation in species with stage-structured life histories.

What was the mechanism behind the intracohort density-dependent mortality of the YOY fish? The mid-season sampling in July 1995 showed that early growth in YOY fathead minnows was density-dependent, and that large differences in density of YOY fish persisted. But, despite these mid-season differences, both mean size and density of surviving YOY at the end of the season were not different between treatments. Taken together, this indicates that density-dependent mortality was still occurring after mid-season and that this mortality was selective. Not only had final mean sizes converged, but the variability of the final size distributions of YOY was related to the mortality rate experienced; at high mortality rates the final size distributions became less variable over

the summer, whereas in populations where YOY mortality was low, a substantial size variation in the YOY cohort remained.

Two commonly important characteristics that can result in selective mortality among YOY fish are size (Post and Prankevicius 1987; Pepin 1993) and growth rate (DeAngelis et al. 1991; Rice et al. 1993). Selection for either of these characteristics (it is difficult to distinguish between them empirically) would have been sufficient to result in the final size distributions that I observed.

The agent of the selective mortality of YOY fish is generally ascribed to either predation (including cannibalism) or starvation. Although laboratory experiments showed that YOY are easily cannibalized by adults in a size-dependent manner (larger adults are able to cannibalize larger fry than smaller adults can, Chapter 3), the lack of a relationship between adult density and YOY mortality does not support this mechanism. A more plausible explanation is that cannibalism was a function of YOY density and size-distribution. Starvation is another likely source of mortality in this experiment; the density-dependent growth that YOY fish were experiencing is often an indication of poor food availability (e.g., Fox et al. 1989), and the probability of starvation also decreases with increasing body size (Miller et al. 1988).

In either case, density-dependent mortality acting during the YOY stage led to strong convergence in cohort size; the range in final densities was reduced from over thirteen-fold initially down to final densities that did not differ between treatments. In fact, there were no treatment differences in either final abundance or average total length of YOY fish. The only exception was the LDA pond half with the highest initial YOY

density, where mortality was so high that the final number of YOY was extremely low (two hundred individuals); this suggests overcompensation by the mechanisms controlling recruitment.

Since final cohort abundance and average length of survivors were strongly regulated during the first season of life, an understanding of the processes occurring during the adult and egg stages may seem unimportant. But this ignores density-dependent differences in the variability of characteristics displayed by individuals, resulting from the selective mortality experienced by the YOY fish, which may be as important as the average characters in controlling recruitment, i.e. it is often the non-average individual that survives (DeAngelis et al. 1991; Crowder et al. 1992; Rice et al. 1993). For fatheads, variability of the final YOY size distribution, and perhaps final YOY condition, were related to initial YOY density. If mortality was highest during the egg stage (HDA), producing a low density of YOY fish, then mortality during the YOY fish stage was very low with little selection for size or growth rate. Conversely, where mortality was low during the egg stage (LDA), the opposite occurred and survivors underwent strong selection. The consequence was that cohorts of YOY undergoing intense selective mortality as an indirect effect of low egg cannibalism were less variable in size than cohorts for which mortality in the YOY stage was less intense.

Indirect evidence indicated that this difference in the amount of size variation could have population-level consequences. Another important source of mortality for YOY fish is the overwinter period, especially for populations near the northern limit of a species range (Shuter and Post 1990). Overwinter mortality can result from depletion of energy

reserves (Post and Evans 1989) and lowered osmoregulatory ability (Johnson and Evans 1996), which are both influenced by body size and condition (with smaller individuals faring worse), as well as the length and severity of the winter. Thus, overwinter stress should have different consequences for populations with the same mean size but different variation in size, as in this experiment. High size variability should be advantageous if a winter is severe because more fish will be at the large extreme of the size distribution. In a less severe winter there may be more survivors in less variable populations, which have few small individuals. Indirect evidence suggested that the 1994-95 winter was severe enough that the variation in size prior to the winter could have had important consequences. The size distribution of fish that successfully overwintered was skewed to the left, and most individuals were >32 mm. Yet in the fall, most of the individuals had been <22 mm. Between these two samples, water temperatures remained <6° C, so growth was unlikely. Assuming that removal of fish in the fall was not selective for smaller individuals, then overwinter mortality was strongly size-selective, with individuals at least 50% larger than the mean size (19 mm) surviving best. Thus, if the experiments had continued over winter, I expect that populations with the highest variability in size among the YOY (HDA) would have had the most survivors in the following spring.

Conclusion

The populations of fathead minnows in my experiment exhibited very strong density-dependent processes. These processes are known to contribute to regulation of fish populations in nature. Populations whose densities differed by four-fold produced cohorts of young that, although differing initially (as eggs) by a factor of thirteen, converged in abundance by the end of their first season of life. However, the different density-dependent processes that operated during this period were stage-specific, and the relative strength of each process was dependent, in a sort of life-history cascade, on the strength of the process(es) acting in the previous stage. Because of the interactions and interdependencies of these stage-specific processes, populations that had different initial densities produced cohorts of young that, although converging in abundance, differed in at least one characteristic (variability in body size). These differences could affect the ultimate recruitment success of this cohort. Studying the density-dependent processes acting during the different life-history stages of stage-structured populations is vital to a full understanding of the dynamics of such populations.

Table 2-1: Summary of analysis of covariance on the effects of the density of stocked fish on proportion of YOY dying, with initial number of YOY as a covariate. For this analysis, R^2=0.986.

Source	Sum of Squares	df	F-ratio	P
Stocked fish density	0.014	1	9.3	0.06
Initial number of YOY (covar.)	0.070	1	41.74	0.008
Error	0.005	3		

Table 2-2: Summary of regression results for final mean size, final condition and coefficient of variation of final size distribution versus initial number of YOY and logit mortality (log (odds of dying)) during their first growing season.

Relationship	Source	Sum of squares	df	F-ratio	P	R^2
mean size vs init. # YOY	regression	3.29	1	0.299	0.61	NS
	residual	44.1	4			
mean size vs logit (dying)	regression	2.38	1	0.212	0.67	NS
	residual	44.9	4			
condition vs init. # YOY	regression	0.0023	1	2.464	0.19	NS
	residual	0.0037	4			
condition vs logit (dying)	regression	0.003	1	3.927	0.118	NS
	residual	0.003	4			
C.V. vs init. # YOY	regression	152.5	1	56.28	0.001	0.93
	residual	10.84	4			
C.V. vs logit (dying)	regression	152.4	1	55.68	0.001	0.93
	residual	10.94	4			

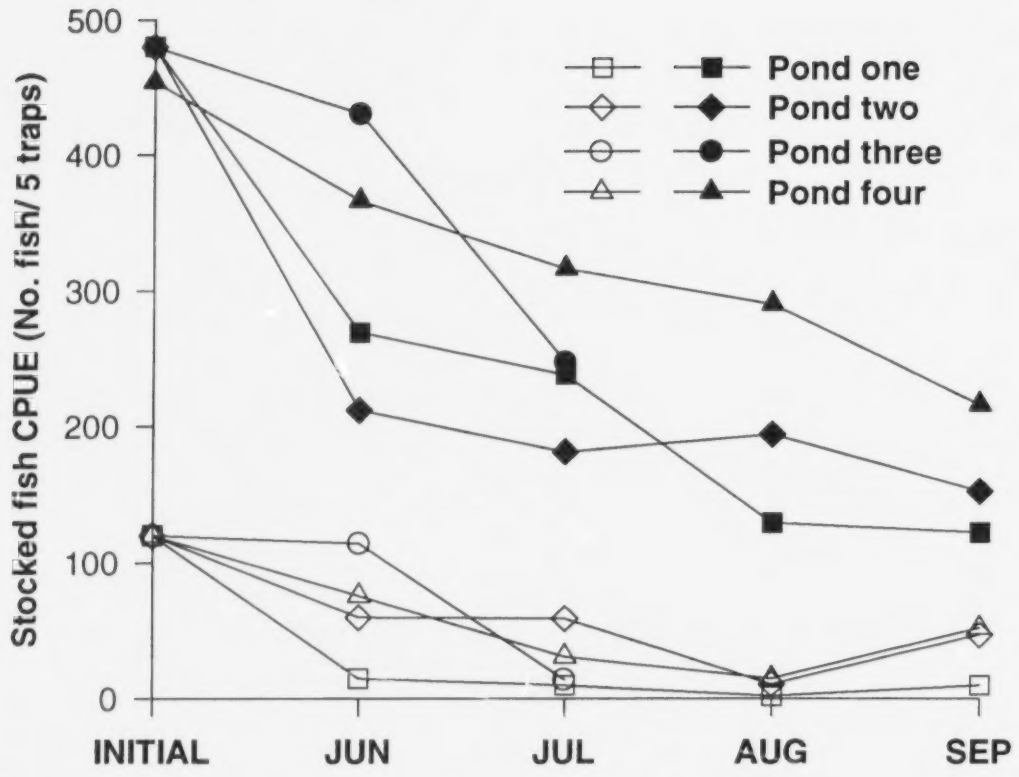

FIG. 2-1. Catch-per-unit-effort (CPUE) of stocked fathead minnows (≥ age-1): number caught in five minnow traps during standardized monthly samplings in each experimental pond. Solid symbols indicate HDA (high density adult) treatments and open symbols are LDA (low density adult) treatments. Note that there are no data for pond three after July, as treatments in this pond were lost due to a flood in mid-August. "Initial" refers to the initial number of fathead minnows stocked.

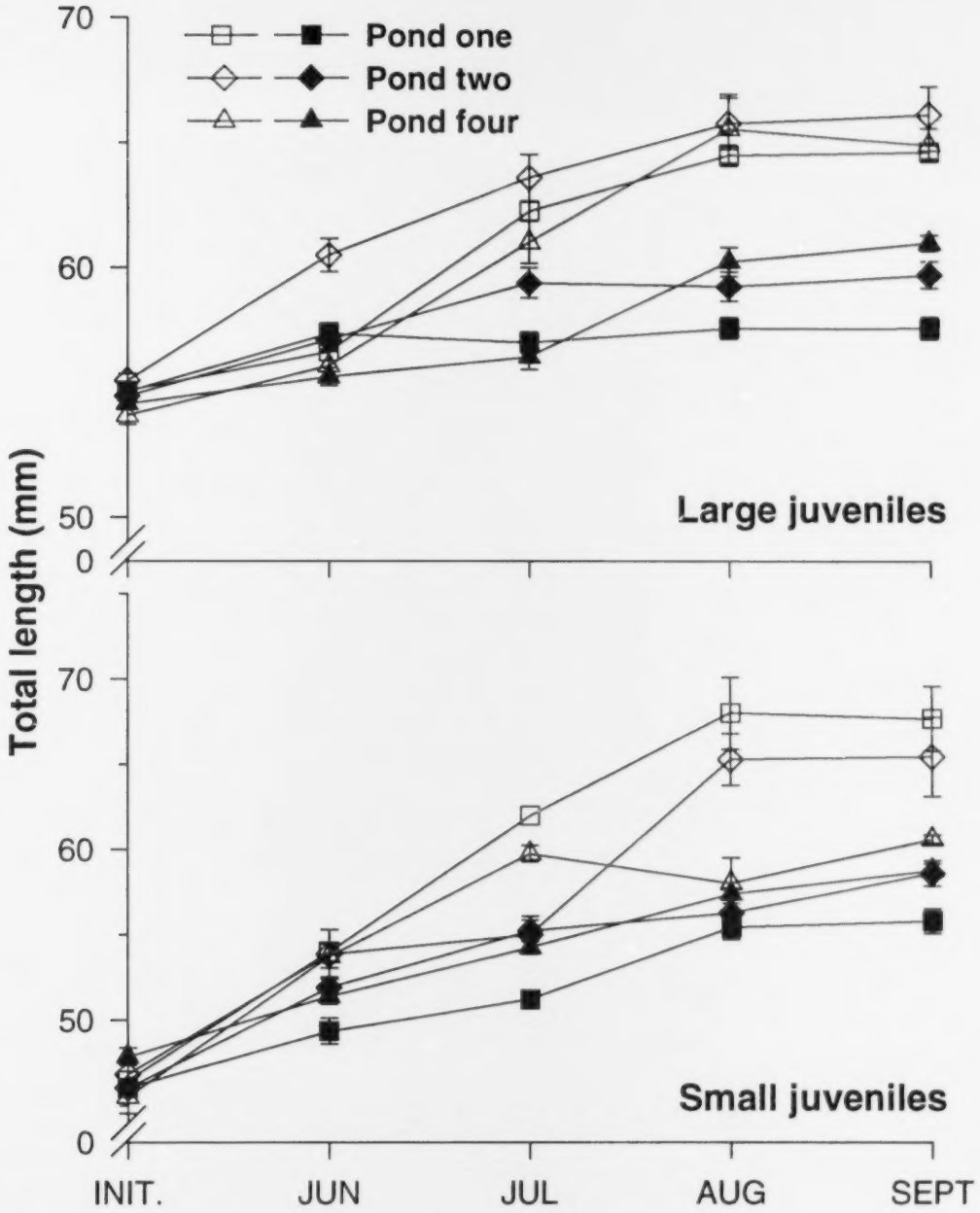

FIG. 2-2. Growth (total length ± SE) of two marked size-classes of juvenile (age-1) fathead minnows stocked into experimental ponds at two different densities (note there are no data for pond three, due to flooding). Solid symbols indicate HDA (high density adult) treatments and open symbols indicate LDA (low density adult) treatments.

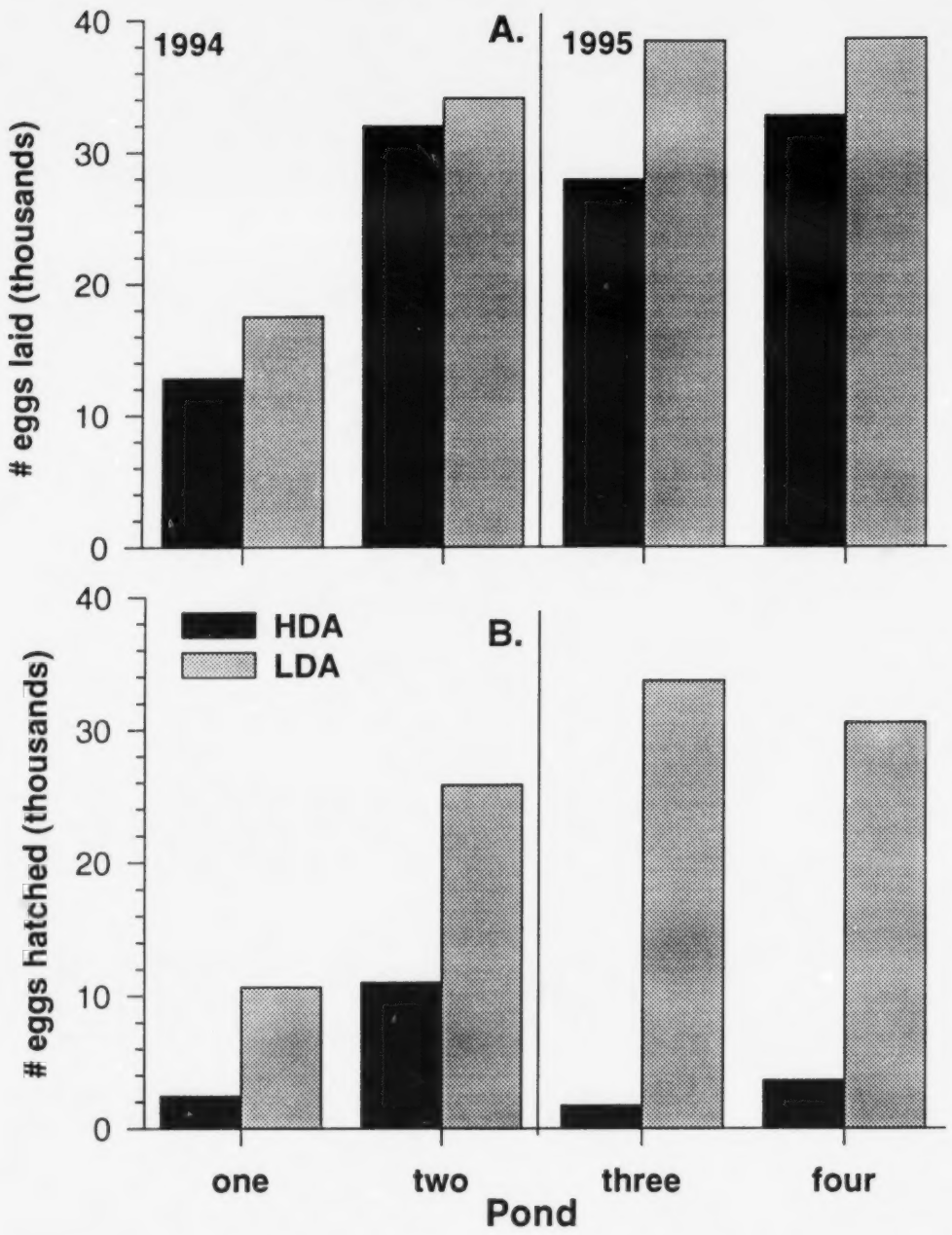

FIG. 2-3.A. Number of eggs laid by stocked fathead minnows in the experimental ponds. B. Number of fathead minnow eggs hatched (=initial number of YOY fish) in all ponds. LDA = low density adult treatment; HDA = high density adult treatment.

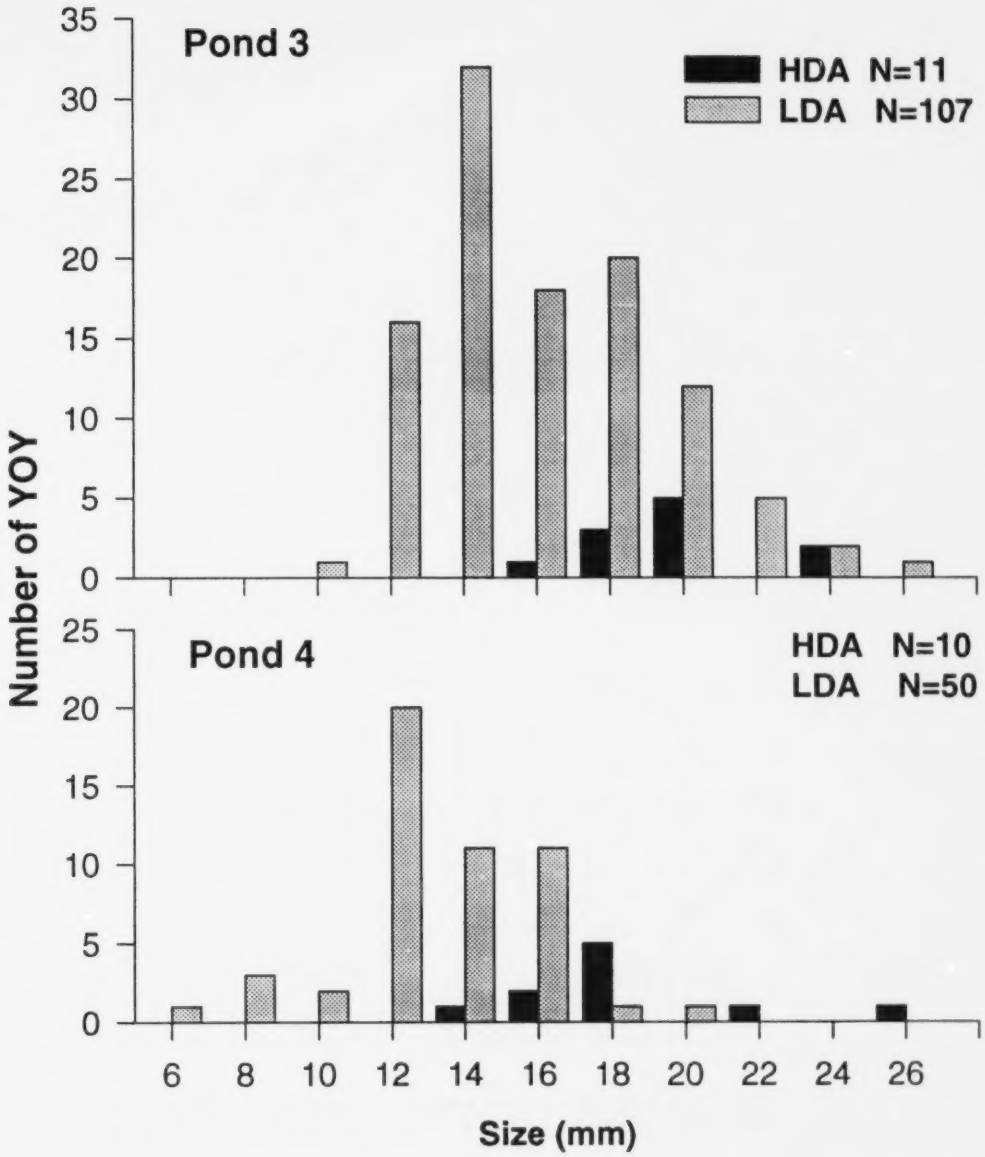

FIG. 2-4. Mid-season (July 15) size distributions of young-of-the-year (YOY) fathead minnows in ponds three and four (1995). LDA = low density adult treatment; HDA = high density adult treatment.

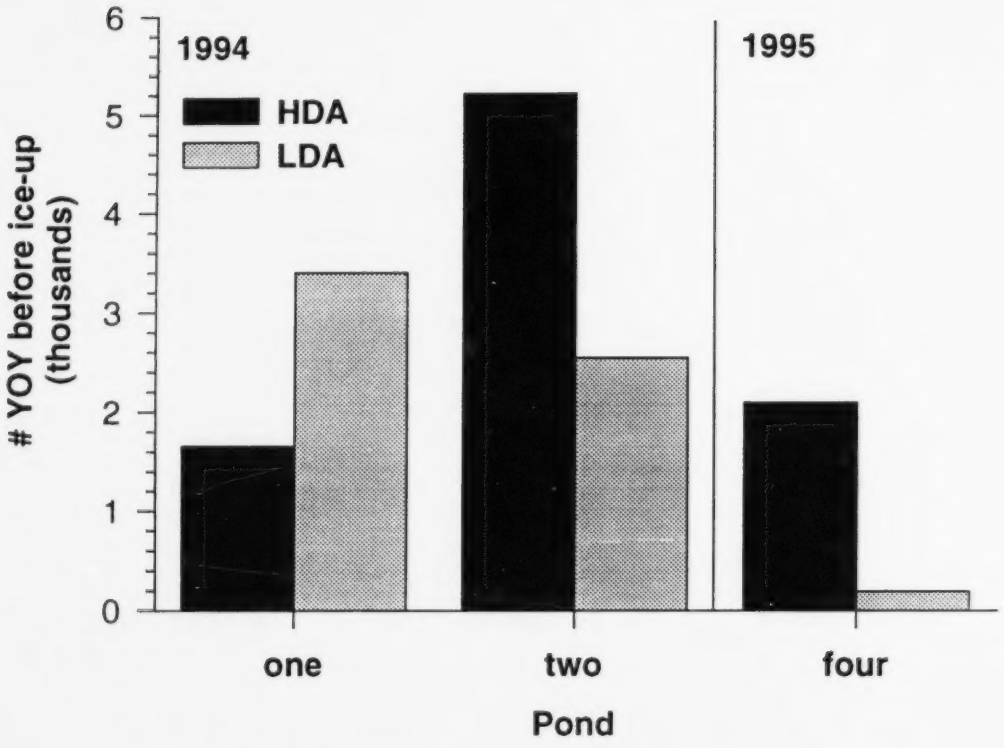

FIG. 2-5. Number of young-of-the-year (YOY) fathead minnows remaining at ice-up. Note there are no data for pond three in 1995, due to flooding. LDA = low density adult treatment; HDA = high density adult treatment.

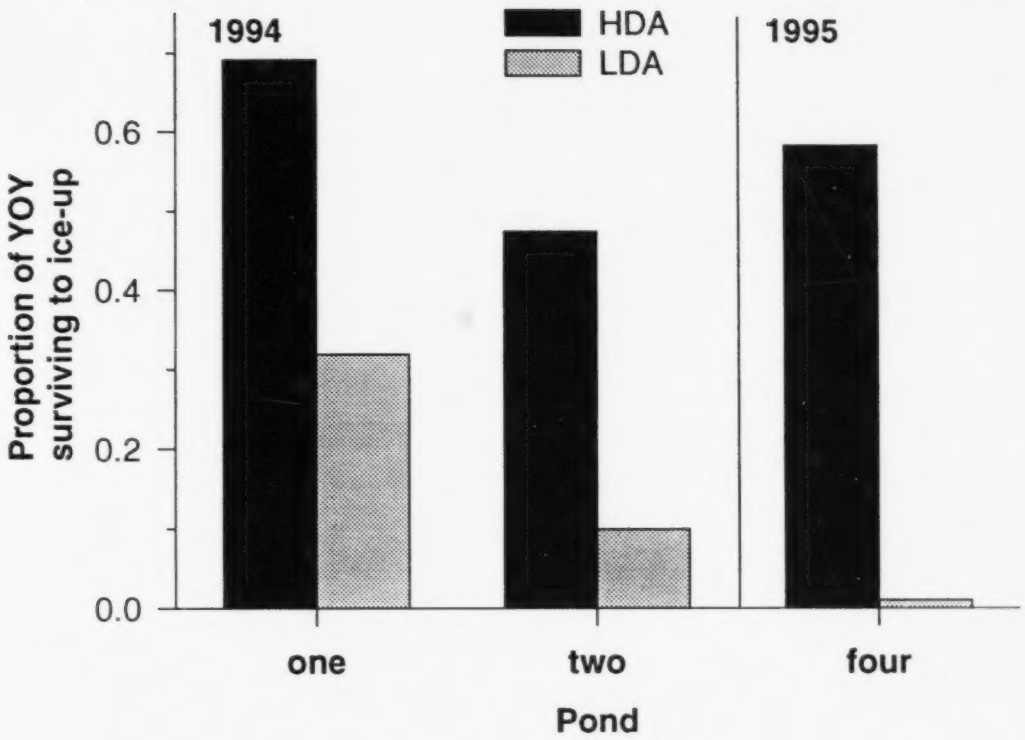

FIG. 2-6. Proportion of young-of-the-year (YOY) fathead minnows that survived until the fall (just prior to ice-up) in all the experimental ponds (except pond three, which was lost in August due to flooding).

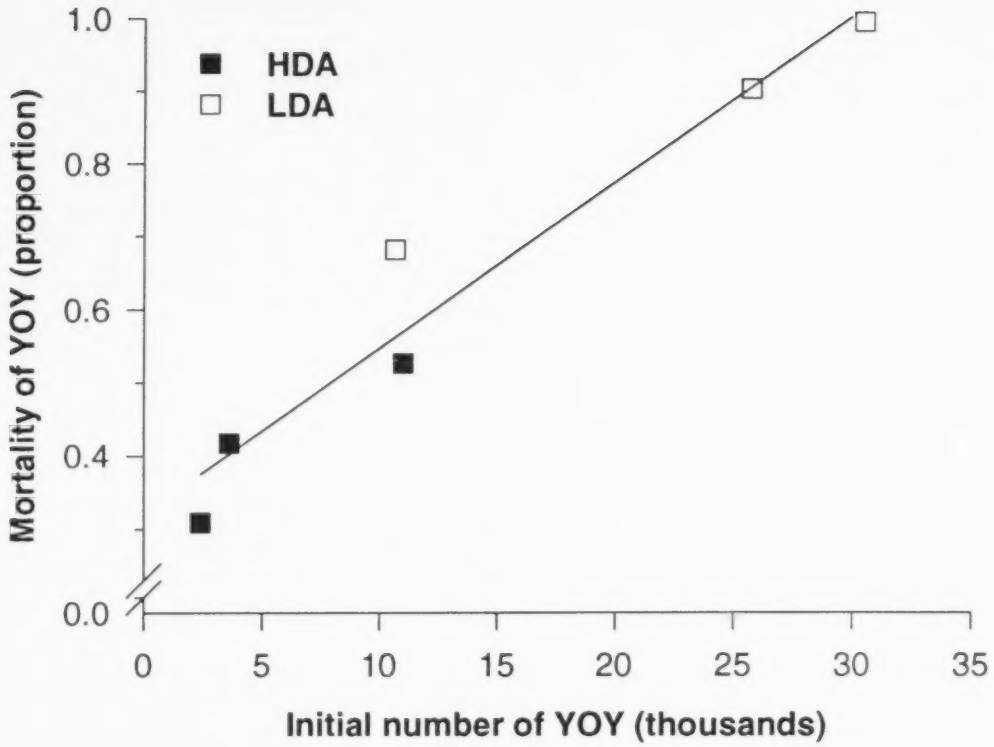

FIG. 2-7. Proportion of young-of-the-year (YOY) fathead minnows dying over the summer as a function of initial number of YOY that hatched (both treatments combined). The regression line equation is: Mort. = 0.32 + 2.27E-5 (init. # YOY); $R^2 = 0.93$. LDA = low density adult treatment; HDA = high density adult treatment.

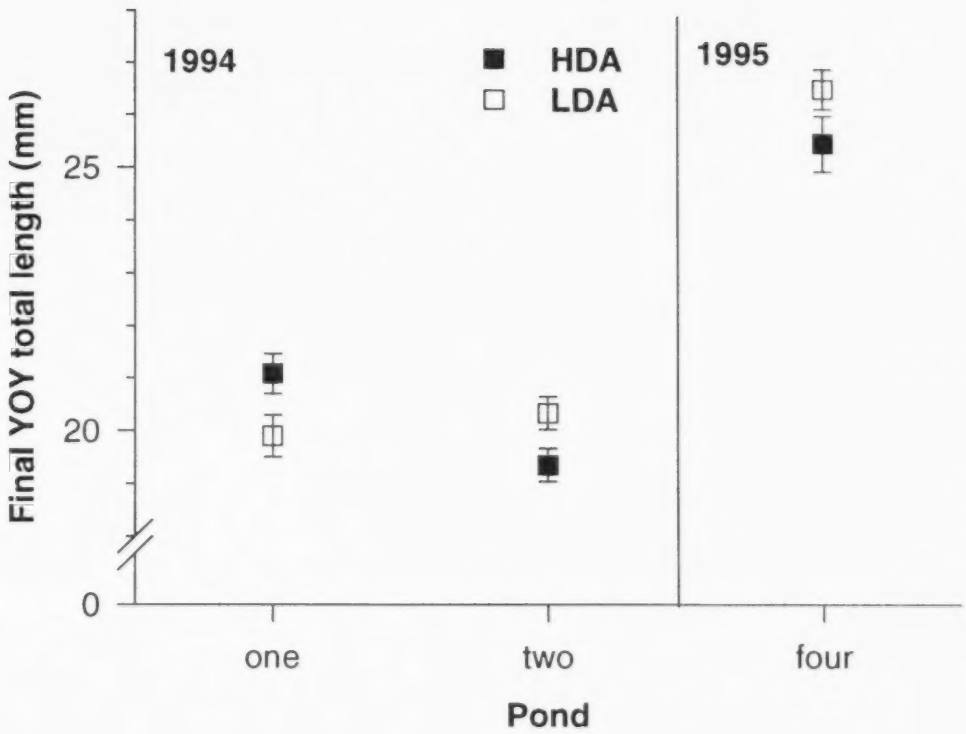

FIG. 2-8. Final mean size (± SE) of young-of-the-year (YOY) fathead minnows, just before ice-up in the experimental ponds (except pond 3, which was lost due to flooding). LDA = low density adult treatment; HDA = high density adult treatment.

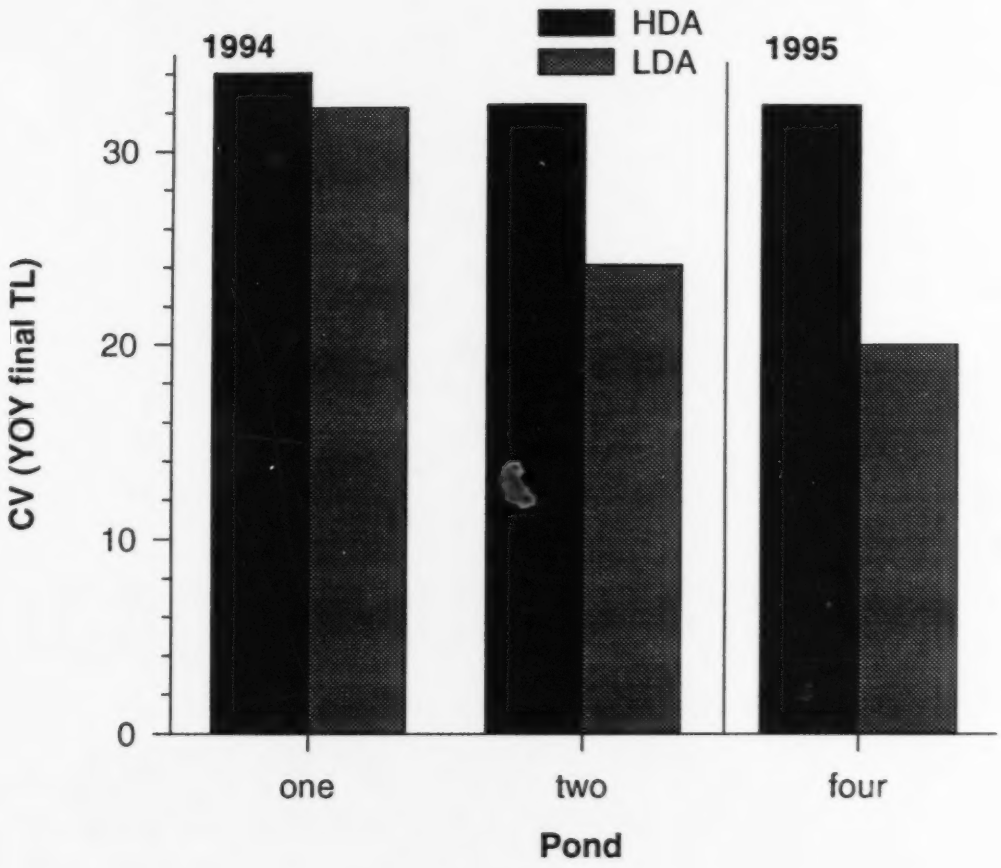

FIG. 2-9. Coefficient of variation of final lengths for young-of-the-year (YOY) fathead minnows for all the experimental ponds (except pond 3, which was lost due to flooding). LDA = low density adult treatment; HDA = high density adult treatment.

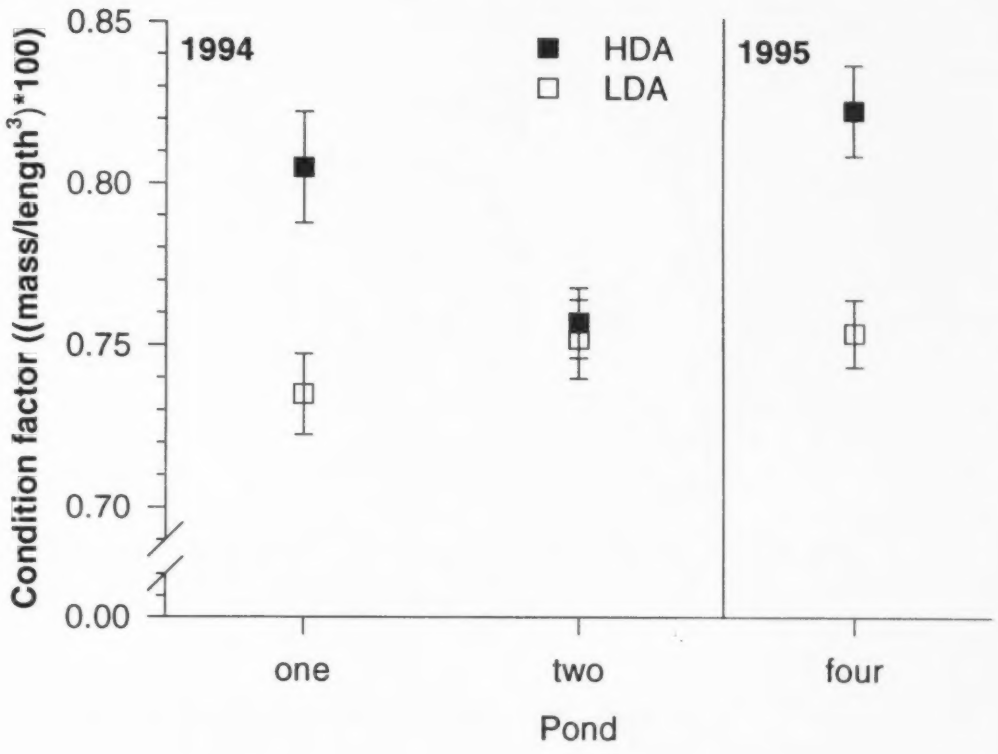

FIG. 2-10. Condition index of young-of-the-year fathead minnows just prior to ice-up in the experimental ponds (except pond 3, which was lost due to flooding). LDA = low density adult treatment; HDA = high density adult treatment.

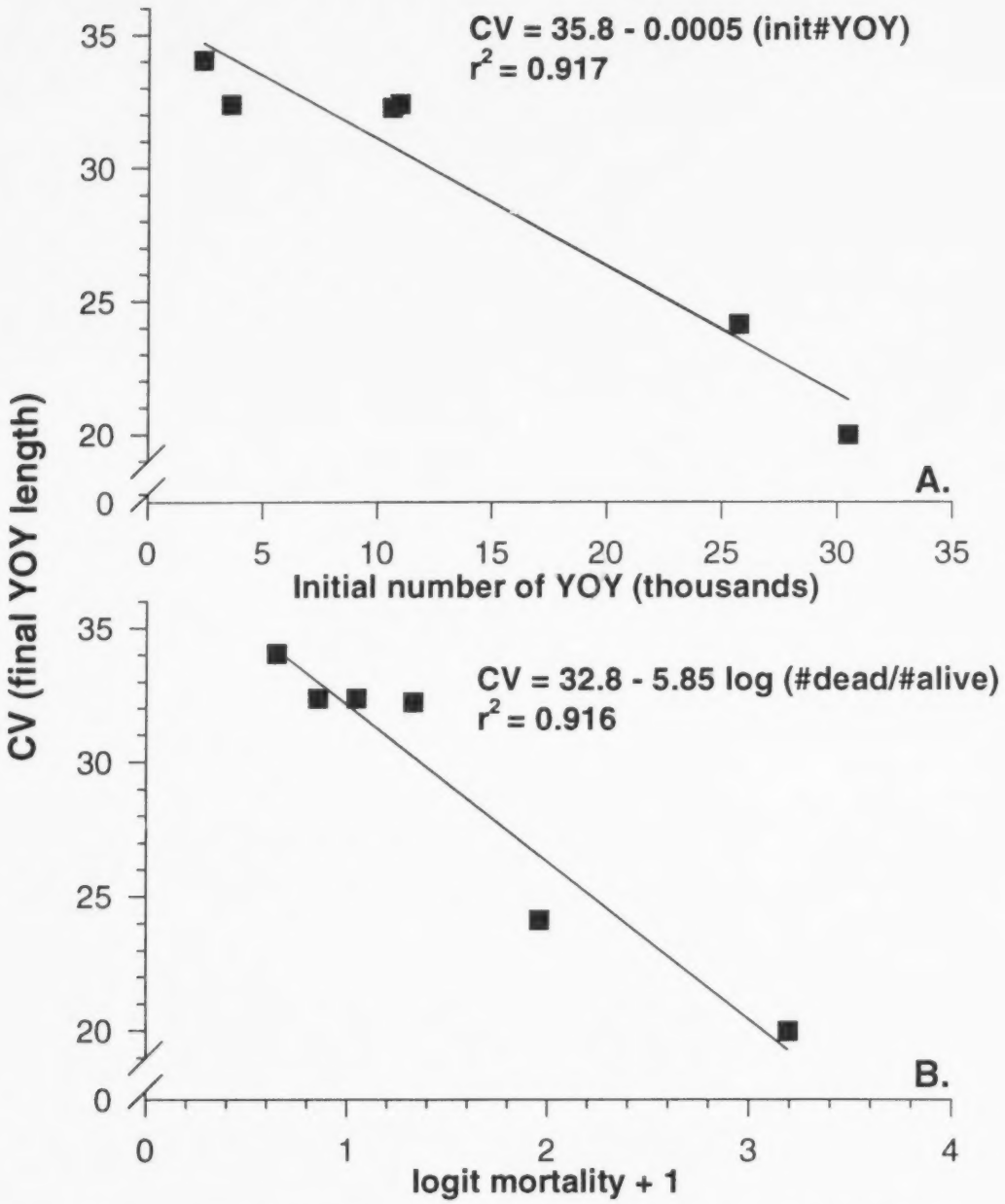

FIG. 2-11.A. Coefficient of variation of final lengths for young-of-the-year (YOY) fish as a function of the initial number of YOY. Line represents a best fit line based on linear regression. B. Coefficient of variation of final lengths for young-of-the-year (YOY) fish as a function of the logit transformed mortality (log (# dead/# alive)). Line represents a best fit line based on linear regression analysis.

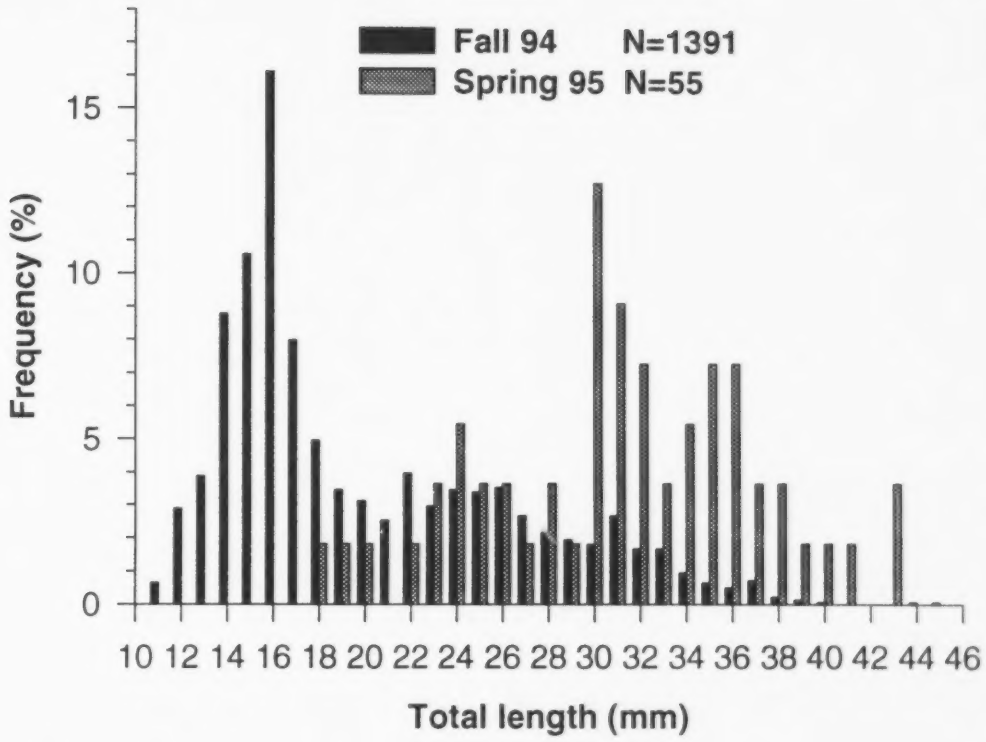

FIG. 2-12. Size distribution of young-of-the-year fathead minnows that had overwintered during 1994-1995 from all ponds (combined), compared with the combined size distribution of YOY fish before ice-up.

LITERATURE CITED

Andrewartha, H. G., and L. C. Birch. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago, Illinois, USA.

Arcese, P. J., N. M. Smith, W. M. Hochachka, C. M. Rogers, and D. Ludwig. 1992. Stability, regulation, and the determination of abundance in an insular song sparrow population. Ecology 73: 805-822.

Barlow, J. 1992. Nonlinear and logistic growth in experimental populations of guppies. Ecology 73: 941-950.

Beverton, R. J. H., and Holt, S. J. 1957. On the dynamics of exploited fish populations. Fisheries Investment Series 2, Volume 19. U. K. Ministry of Agriculture and Fisheries, London, UK.

Brodeur, R. D., K. M. Bailey, and S. Kim. 1991. Cannibalism on eggs by walley pollock *Theragra chalcogramma* in Shelikof Strait, Gulf of Alaska. Marine Ecology Progress Series 71: 207-218.

Cargnelli, L. M., and M. R. Gross. 1996. The temporal dimension in fish recruitment: birth date, body size, and size-dependent survival in sunfish (bluegill: *Lepomis macrochirus*). Canadian Journal of Fisheries and Aquatic Sciences 53: 360-367.

Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. BioScience 35: 634-639.

Charnov, E. L. 1986. Life history evolution in a 'recruitment population': why are adult mortality rates constant? Oikos 47: 29-134.

Crowder, L. B., J. A. Rice, T. J. Miller, and E. A. Marschall. 1992. Empirical and theoretical approaches to size-based interactions and recruitment variability in fishes. Pages 237-255 *in* D. L. DeAngelis and L. J. Gross, editors. Individual-based approaches in ecology: concepts and individual models. Chapman and Hall, New York, New York, USA.

Cushing, D. H. 1981. Fisheries biology, a study in population dynamics. University of Wisconsin Press, Madison, Wisconsin, USA.

DeAngelis, D. L., L. Godbout, and B. J. Shuter. 1991. An individual-based approach to predicting density-dependent dynamics in smallmouth bass populations. Ecological Modelling 57: 91-115.

Den Boer, P. J. 1968. Spreading of risk and stabilization of animal numbers. Acta Biotheoretica 18: 165-194.

Dominey, W. J., and L. S. Blumer. 1984. Cannibalism of early life stages in fishes. Pages 43-64 *in* G. Huasfater and S. B. Hrdy, editors. Infanticide. Aldene, New York, New York, USA.

Elliot, J. M. 1989. Mechanisms responsible for population regulation in young migratory trout, *Salmo trutta*. I. The critical time for survival. Journal of Animal Ecology 58: 987-1001.

Fox, M. G. 1994. Growth, density, and interspecific influences on pumpkinseed sunfish life histories. Ecology 75: 1157-1171.

Fox, M. G., and D. D. Flowers. 1990. Effect of fish density on growth, survival, and food consumption by juvenile walleyes in rearing ponds. Transactions of the American Fisheries Society 119: 112-121.

Fox, M. G., J. A. Keast, and R. L. Swainson. 1989. The effect of fertilization regime on juvenile walleye growth and prey utilization in rearing ponds. Environmental Biology of Fishes 26: 131-144.

Gale, W. F., and G. L. Buynak. 1982. Fecundity and spawning frequency of the fathead minnow - a fractional spawner. Transactions of the American Fisheries Society 111: 35-40.

Godfray, H. C. J., and M. P. Hassell. 1992. Long time series reveal density dependence. Nature 359: 673-674.

Hamrin, S. F., and L. Persson. 1986. Asymmetrical competition between age classes as a factor causing population oscillations in an obligate planktivorous fish species. Oikos 47: 223-232.

Harris, R. N. 1987. An experimental study of population regulation in the salamander, *Notophthalmus viridescens* dorsalis (Urodela: Salamandridae). Oecologia 71: 280-285.

Held, J. W., and J. J. Peterka. 1974. Age, growth and food habits of the fathead minnow, *Pimephales promelas*, in North Dakota saline lakes. Transactions of the American Fisheries Association 4: 743-755.

Hill, C. 1992. Interactions between year classes in the benthic amphipod *Monoporeia affinis*: effects on juvenile survival and growth. Oecologia 91: 157-162.

Hopper, K. R., P. H. Crowley, and D. Kielman. 1996. Density dependence, hatching synchrony, and within-cohort cannibalism in young dragonfly larvae. Ecology 77: 191-200.

Hovenkamp, F. 1992. Growth-dependent mortality of larval plaice *Pleuronectes platessa* in the North Sea. Marine Ecology Progress Series 82: 95-101.

Hyatt, K. D., and N. H. Ringler. 1989. Role of nest raiding and egg predation in regulating population density of threespine sticklebacks (*Gasterosteus aculeatus*) in a coastal British Columbia lake. Canadian Journal of Fisheries and Aquatic Sciences 46: 372-383.

Johnson, T. B., and D. O. Evans. 1996. Temperature constraints on overwinter survival of age-0 white perch. Transactions of the American Fisheries Society 125: 466-471.

Litvak, M. K., and W. C. Leggett. 1992. Age and size-selective predation on larval fishes: the bigger-is-better hypothesis revisited. Marine Ecology Progress Series 81: 13-24.

Mappes, J., and A. Kaitala. 1994. Experiments with *Elasmucha grisea* L. (Heteroptera: Acanthosomatidae): does a female parent bug lay as many eggs as she can defend? Behavioral Ecology 5: 314-317.

Maret, T. J., and J. P. Collins. 1996. Effect of prey vulnerability on population size-structure of a gape-limited predator. Ecology 77: 320-324.

Margulies, D. 1990. Vulnerability of larval white perch, *Morone americana*, to fish predation. Environmental Biology of Fishes 27: 187-200.

Markus, H. 1934. Life-history of the blackhead minnow (*Pimephales promelas*) Copeia 1934: 116-122.

McMenemy, J. R. 1995. Survival of Atlantic salmon fry stocked at low density in the West River, Vermont. North American Journal of Fisheries Management 15: 366-374.

McMillan, V. E., and R. J. F. Smith. 1974. Agonistic and reproductive behaviour of the fathead minnow (*Pimephales promelas* Rafinesque). Zeitschrift für Tierpsychologie 34: 25-58.

Miller, T. J., L. B. Crowder, J. A. Rice, and E. A. Marschall. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. Canadian Journal of Fisheries and Aquatic Sciences 45: 1657-1670.

Myers, R. A., and N. G. Cadigan. 1993. Density-dependent juvenile mortality in marine demersal fish. Canadian Journal of Fisheries and Aquatic Sciences 50: 1576-1590.

Nagel, T. 1976. Technique for collecting newly hatched fathead minnow fry. The Progressive Fish-Culturist 38: 137.

Nicholson, A. J. 1933. The balance of animal populations. Journal of Animal Ecology 2: 132-178.

Pepin, P. 1993. An appraisal of the size-dependent mortality hypothesis for larval fish: comparison of a multispecies study with an empirical review. Canadian Journal of Fisheries and Aquatic Sciences 50: 2166-2174.

Polis, G. A. 1981. The evolution and dynamics of intraspecific predation. Annual Review of Ecology and Systematics 12: 225-251.

Post, J. R., and D. O. Evans. 1989. Size-dependent overwinter mortality of young-of-the-year yellow perch (*Perca flavescens*): laboratory, in situ enclosure, and field experiments. Canadian Journal of Fisheries and Aquatic Sciences 46: 1958-1968.

Post, J. R., and A. B. Prankevicius. 1987. Size-selective mortality in young-of-the-year yellow perch (*Perca flavescens*): evidence from otolith microstructure. Canadian Journal of Fisheries and Aquatic Sciences 44: 1840-1847.

Price, C. J., W. M. Tonn, and C. A. Paszkowski. 1991. Intraspecific patterns of resource use by fathead minnows in a small boreal lake. Canadian Journal of Zoology 69: 2109-2115.

Rice, J. A., L. B. Crowder, and M. E. Holey. 1987. Exploration of mechanisms regulating larval survival in Lake Michigan bloater: a recruitment analysis based on characteristics of individual larvae. Transactions of the American Fisheries Society 116: 703-718.

Rice, J. A., T. J. Miller, K. A. Rose, L. B. Crowder, E. A. Marschall, A. S. Trebitz, and D. L. DeAngelis. 1993. Growth rate variation and larval survival: inferences from an individual-based size dependent predation model. Canadian Journal of Fisheries and Aquatic Sciences 50: 133-142.

Ricker, W. E. 1954. Stock and recruitment. Journal of the Fisheries Research Board of Canada 11: 559-623.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Fisheries Research Board of Canada, Ottawa, Canada, Bulletin No. 191.

Robinson, C. K., and W. M. Tonn. 1989. Influence of environmental factors and piscivory in structuring fish assemblages of small Alberta lakes. Canadian Journal of Fisheries and Aquatic Sciences 46: 81-89.

Schultz, E. T. 1993. The effect of birth date on fitness of female dwarf perch, *Micrometrus minimus* (Perciformes: Embiotocidae). Evolution 47: 520-539.

Scott, W. B., and E. J. Crossman. 1973. Freshwater Fishes of Canada. Department of Fisheries and Oceans, Ottawa, Ontario, Canada.

Shuter, B. J., and J. R. Post. 1990. Climate, population variability, and the zoogeography of temperate fishes. Transactions of the American Fisheries Society 119:314-336.

Sinclair, A. R. E. 1989. Population regulation in animals. Pages 197-241 *in* J. M. Cherrett, editor. Ecological concepts. Blackwell Scientific, Oxford, UK.

Smith, C., and P. Reay. 1991. Cannibalism in teleost fish. Reviews in Fish Biology and Fisheries 1: 41-64.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry: Second Edition. W.H. Freeman and Company, San Francisco, California, USA.

Tonn, W. M., I. M. Holopainen, and C. A. Paszkowski. 1994. Density-dependent effects and the regulation of crucian carp populations in single-species ponds. Ecology 75: 824-834.

Turchin, P. 1995. Population regulation: old arguments and a new synthesis. Pages 19-37 *in* N. Cappuccino and P. W. Price, editors. Population dynamics: new approaches and synthesis. Academic Press Inc., New York, New York, USA.

Unger, L. M. 1983. Nest defense by deceit in the fathead minnow, *Pimephales promelas*. Behavioral Ecology and Sociobiology 13: 125-130.

Valdes Szeinfeld, E. S., and K. L. Cochrane. 1992. The potential effects of cannibalism and intraguild predation on anchovy recruitment and clupeoid fluctuations. South African Journal of Marine Science 2: 695-702.

Whoriskey, F. G. and G. J. FitzGerald. 1985. Sex, cannibalism and sticklebacks. Behavioural Ecology and Sociobiology 18: 15-18.

Wilkinson, L. 1992. SYSTAT: the System for Statistics. Systat Inc., Evanston, Illinois, USA.

Wootton, R. J. 1990. Ecology of teleost fishes. Chapman & Hall, London, UK.

CHAPTER 3

CONSEQUENCES OF SIZE VARIATION TO SURVIVAL OF YOUNG-OF-THE-YEAR FATHEAD MINNOWS (*PIMEPHALES PROMELAS*)

INTRODUCTION

For many organisms it is commonly thought that the regulation of population size has its roots in processes acting during early life history (Miller et al. 1988; Elliot 1989; Arcese et al. 1992), yet despite decades of research, the processes that control recruitment in animal populations are still poorly understood. Recently, understanding of these processes has been furthered by explicitly considering differences between individuals in characteristics such as size, age or growth rate (Huston et al. 1988; DeAngelis and Gross 1992; VanWinkle et al. 1993). This approach has its basis in the idea that probability of survival can vary substantially among members of a cohort due to differences in these characteristics (Rice et al. 1993a). Recent studies indicate that these differences can be very important in determining both the number and characteristics of survivors (Rice et al. 1993b; Hopper et al. 1996; Maret and Collins 1996). Still, the question of how these differences affect recruitment remains largely unanswered, especially from an empirical standpoint.

Explicitly considering differences in characteristics may be especially important in populations where such differences are substantial and where survival is related to those characteristics (Rice et al. 1993b). For example, differences in size often arise in populations with asynchronous hatching and/or indeterminate growth and may be

accentuated by competition (Rubenstein 1981) or other processes that cause unequal food intake (Lomnicki 1988). In turn, body size has been related to survival in, e.g., amphibians (Harris 1987; Maret and Collins 1994), insects (O'Neill 1992; VanBuskirk 1989) and fish (Post and Prankevicius 1987; Miller et al. 1988; Margulies 1990; Litvak and Leggett 1992).

Several studies have recently suggested that in populations with size-dependent mortality, intra-cohort variation in initial size, age, or growth rate can have dramatic effects on the number and characteristics of individuals that subsequently survive. Simulations using an individual-based model of larval bloater (*Coregonus hoyi*) predicted that increased growth rate variation in cohorts would increase survival and size of survivors in a system with size-dependent predation (Rice et al. 1993b). In contrast, two laboratory-based studies on larval fish found that increased initial variation in age (Ellis et al. 1993) and size (Folkvord and Ottera 1993) increased the mortality rate. Recent studies with invertebrates (Hopper et al. 1996) and amphibians (Maret and Collins 1996) also suggested that initial size variation interacts with size-dependent predation to increase mortality rate. In the first case (Rice et al. 1993b), mortality was the result of an inter-specific predator, whereas mortality in the other cases was due to intracohort cannibalism, whose rates increased with increased variance in size or age. However, these studies involved either simulations or laboratory experiments in which no other life stages were present and artificial food sources were used. These studies also relied on initial variation, but it has been predicted that selective survival among young occurs primarily after differences have been established (Rice et al. 1993b). Thus, the applicability of these

results to situations with more natural conditions of food availability, temperature and light regimes, and the presence of other age-classes, remains to be tested.

To determine if variation in size-distributions of young-of-the-year (YOY) fish is important for recruitment under more natural conditions I stocked outdoor pond enclosures with either narrow or wide size distributions of YOY fathead minnows (*Pimephales promelas*) in the presence of potentially cannibalistic adults, and monitored survival and growth of YOY over a 63-d period. In contrast, mean sizes (which were the same as those in nearby natural ponds on August 1) and densities of these YOY did not differ initially among enclosures. To determine what sizes of YOY fish were vulnerable to cannibalism by different sizes of older fish, I also conducted laboratory feeding experiments with juvenile and adult fathead minnows. My objective was to see if variation in the mid-season size distribution of fathead minnows could interact with size-dependent mortality (gape-limited cannibalism by adults) to affect the number and characteristics of the YOY fish that survived to the end of the first growing season.

METHODS AND MATERIALS

Natural History

The fathead minnow is a small-bodied fish widely distributed in North America. In the boreal region of Alberta, which is the northwestern limit of its range (Scott and Crossman 1973), the fathead minnow is common in small lakes and ponds, where it can occur both with and without other small-bodied species (Robinson and Tonn 1989). These fish typically require three summers to reach maturity in Alberta, compared with one or two

summers at lower latitudes (Held and Peterka 1974). Published diets of these minnows describe a combination of algae, detritus and small invertebrates (Price et al. 1991), with the latter having the highest nutritional quality. Fathead minnow adults have been observed to cannibalize both their eggs (Unger 1983; chapter 2) and larval fish (personal observation) in laboratory settings. Because the breeding season can be extensive (late May to early August), a broad range of sizes of young naturally coexist throughout the summer. Fathead minnows are hardy, and all life stages are easy to collect from natural ponds and keep alive, making it an ideal species for a manipulative experiment of this sort.

Location

All experiments were conducted at the University of Alberta's Meanook Biological Research Station (54°37'N, 113°35'W), which is located near the southern limit of the boreal forest region of north-central Alberta, Canada.

Experiment I: Vulnerability of YOY to cannibalism

This experiment was designed to determine what sizes of YOY fish could be either eaten whole, or at least killed, by different size-classes of older life stages (≥ age-1) of fathead minnows. Fish were collected from a nearby lake, using Gee minnow traps for older fish and sweep nets to catch YOY. The older fish (called adults from here on) were separated into four 5-mm size-classes (50-69 mm TL) plus a fifth size-class of fish ≥70 mm TL; YOY fish were separated into 2-mm size-classes between 10mm and 30mm TL. After collecting and sorting, all fish were kept in holding tanks for at least 2 d before the experiments were initiated so that any fish damaged by handling could be identified and removed. Adult fish were starved for 24 h prior to being used in the experiments, whereas

YOY fish were fed *ad libitum* with *Artemia* nauplii. The experimental aquaria (6 L, glass-sided) were set up in randomized blocks of 15, so that each adult size-class could be tested three times with a given size-class of YOY during each run.

Two adults of a single size-class were introduced into each experimental aquarium at least 3 h prior to the experiment. A trial began when five YOY fish of a given size-class were added to each of the experimental aquaria. Aquaria were checked after 20 min and the state of the YOY (dead, alive or consumed) was recorded. At the end of 60 min all remaining fish were removed and counted, and dead, but not consumed, YOY fish were examined for damage.

I began by introducing the smallest size-class of YOY to each of the adult size-classes. If adults from a given size-class were able to eat this size of fish then the next larger size-class of YOY was presented in the next run of the experiment. The experiment was continued in this way until each adult size-class could not either eat or kill any YOY of a size-class in three different runs. In this way I was able to determine the largest size-class of YOY that a given size-class of adults was able to eat or at least attack and kill. Different adults were used for each run, but YOY fish left alive and undamaged were reused because of the paucity of YOY available.

The ratios between adult size (using the mean size of adults in the class) and the maximum size of YOY that those adults could consume were computed for each of the five adult size-classes and compared with the size ratios involving YOY that were killed but not consumed, to see if cannibalism on YOY is size-dependent.

Experiment II: Consequences of size variation

This experiment was run in a set of six enclosures (2.5m x 2.5m x0.75m deep) set within a large experimental pond. Enclosure walls were made of an impermeable polyvinyl material and were attached to wooden frames that were dug into the sandy substrate. A 15cm X 15cm mesh window (500 μm) in one of the walls of each enclosure allowed for the regulation of water levels but otherwise prevented passage of fish and the majority of their planktonic prey. Enclosures had been set up and filled with natural pond water pumped from a nearby dugout 2.5 mo prior to the experiment so that by the beginning of the experiment each enclosure had self sustaining populations of zooplankton and algae (personal observation). Five cattails (*Typha* sp.) were planted in one corner of each of the enclosures to provide structure. YOY fathead minnows were collected, using tow nets and sweep nets, from nearby lakes and were separated by size in the laboratory. All fry were held in aquaria for at least 2 d prior to the experiment so that individuals damaged by handling could be removed.

I added populations of fry to the six enclosures on August 1, 1994. There were two types of populations, with three replicates of each. These populations had the same initial number (160) and mean size (20.5mm) but differed in their size distributions. One population type had a narrow size distribution (all individuals were +/- 1.5mm of the mean) and the other a wide size distribution (+/- 5mm). Four adult males (>70mm) were added to each population as potential predators, providing a density similar to a population in a nearby natural pond where adults were in good health and exhibiting

substantial growth (W. Tonn unpublished data), while ensuring that no reproduction occurred during the experiment.

On October 2nd (Day 63) all fish remaining in the enclosures were removed by electrofishing. These fish were preserved in 95 % ethanol and subsequently counted and measured.

Analysis

I compared final sizes of YOY in the two treatments using the Mann-Whitney U-test. The coefficient of variation (CV) of the size distributions of the surviving fish were compared similarly. Finally, to compare the change in variability between treatments (since the populations had very different initial distributions), I subtracted the initial coefficient of variation from the final in each replicate and compared the magnitude of the change using the Mann-Whitney U-test.

All statistical analyses used are outlined in Sokal and Rohlf (1981). Analyses were performed using the statistical analysis program Systat (version 5.0 for Windows; Wilkinson 1992).

RESULTS

Experiment I: Vulnerability of YOY to cannibalism

Fathead minnows were found to be gape-limited predators on the YOY fish; each size-class of adults had a maximum prey size above which the YOY could not be consumed and larger fish were able to cannibalize progressively larger fry (Table 3-1). None of the size-classes of adults were able to eat fry larger than 19mm TL, but all fish

tested were able to eat fry of 11mm TL. Each group of adults also killed, but could not wholly consume, YOY 1-2mm larger than their maximum prey size. The size-class of adults used in the enclosure experiment was able to attack and kill YOY fish 21 mm TL. The mean ratio of cannibal size to maximum YOY size was 4.2:1 for YOY eaten whole and 3.8:1 for YOY killed but not wholly consumed (Fig. 3-1).

Experiment II: Consequences of size variation

In the pond enclosures, the survival of YOY was significantly higher in the treatment with the initially narrow size distribution (57%) than in the treatment with the wide initial size distribution (40%) (Mann Whitney U -test statistic=9, n=3, P=0.046; Fig. 3-2). The YOY fatheads from the initially less variable populations were slightly but not significantly larger at the end of the season than the fish from the initially more variable population (Mann Whitney U-test statistic=7, n=3, P=0.28; Fig. 3-3).

Despite the large initial differences in the amount of variation in the size-distributions there was no significant difference between treatments in the coefficient of variation of the final size-distributions (Mann Whitney U-test statistic=3, n=3, P=0.513; Fig. 3-4). The initially uniformly sized populations became more variable over the course of the experiment, whereas the populations with high initial variation in size showed little or no change. The change in variability, as measured by the difference between the initial and final coefficient of variation, was significantly different between the two treatments (Mann-Whitney U test statistic= 9, n=3, P=0.05).

DISCUSSION

Laboratory experiments and modeling studies have indicated that the amount of variation among individuals in a population or cohort can be important in determining the number and characteristics of individuals that survive major mortality periods; this should be especially important when mortality is selective with respect to these characteristics (Rice et al. 1993b). If true, then variation in body size should be a key characteristic affecting recruitment of a cohort of YOY fish. Not only does size have the potential to vary substantially within cohorts of larval fish, due to factors such as asynchronous hatching and differential growth rates, but mortality among YOY fish is also often size-selective, as smaller fish display both competitive disadvantages (Miller et al. 1988) and increased vulnerability to: starvation (Rice et al. 1987), overwinter mortality (Post and Evans 1989; Johnson and Evans 1996), and predation (Post and Prankevicius 1987; Rice et al. 1987; Miller et al. 1988).

For fathead minnows, which typically occur in systems lacking piscivorous fish, and frequently lacking any other fish species, cannibalism on both eggs (chapter 2) and larvae may be an important early source of mortality. I have now demonstrated that cannibalism is size-dependent in fathead minnows; the relative size between cannibal and prey appears to determine prey vulnerability, with YOY larger than about 20 mm being completely invulnerable to even the largest adult. Although this threshold size corresponded to the mean size of the YOY in both treatments, the populations with a more variable size-distribution would have more fish in the small extreme (13-15mm), and

these fish would be more vulnerable than the fish in the less variable treatment, all of which were at, or within 1.5 mm of, the invulnerable size.

The interaction between the initial variability of characteristics and the intensity of selective mortality related to these characteristics will help determine the number of individuals that survive. Past laboratory experiments have found that increasing variation in characteristics important to survival (age, size, hatch synchrony) decreases overall survival by increasing the rate of the selective mortality (Ellis et al. 1993; Folkvord and Ottera 1993; Hopper et al. 1996; Maret and Collins 1994). In contrast, an individual-based model (IBM) suggests that increasing variation in larval fish growth rates actually increases overall survival (Rice et al. 1993b). The reason for these seemingly contradictory results can be explained by the sources of mortality. In the laboratory experiments mortality was primarily the result of intracohort cannibalism; under these conditions increasing size variation would increase the relative size difference between cannibals and potential prey, thus decreasing overall survival. In the IBM study, mortality was due to interspecific predation, with all larvae being initially vulnerable; here, any increases in size variation would reduce vulnerability for at least part of the cohort (the larger fish) and thus increase overall survival. Although inter-cohort cannibalism should generally be more similar to interspecific predation than intra-cohort cannibalism, I found that increasing size variation decreased survival among YOY fathead minnows. But, because the YOY I used were from mid-season, rather than newly hatched, many were already invulnerable to predation by adults. Therefore, the treatments with the more variable size-distributions had a higher proportion of fish farther from the threshold size,

which would be both more vulnerable to size-selective cannibalism initially and would take longer to outgrow their vulnerability.

The interaction between initial variability and selective mortality may also control the final amount of variability in characteristics. Increasing the intensity of selection for certain characteristics should tighten the final distribution in the population, e.g., size-selective cannibalism (related to relative size between cannibal and prey) has been predicted to tighten the final size distributions of the prey (Dong and Polis 1992). If mortality is more random, on the other hand, the distribution should become more variable due to stochastic factors acting on those characteristics throughout the season (Huston and DeAngelis 1988). The former prediction has received empirical support (Hopper et al. 1996); the only exception was if the selective mortality source was intracohort cannibalism, in which case the unequal partitioning of food between cannibals (eating members of their cohort) and non-cannibals (eating alternate prey) tended to increase variability of final sizes (Maret and Collins 1996).

In my enclosures, the size distributions of YOY fish became substantially more variable in the populations with low initial size variation but slightly less variable in the high size variation treatment. This suggests that the mortality was more selective in the high variability treatment than in the low variability treatment, which is consistent with the idea that mortality in the high variance treatments, but not the low variance treatment, was at least partly due to size-selective cannibalism. Rice et al. (1993b) also found that mortality was much more selective in variable cohorts than in cohorts with lower variation. Since the size-distributions of my populations with low initial variability

became more variable over the course of the 63-d experiment, it seems likely that survival was more random than selective. It may well be that for mortality to be strongly selective, substantial variation must already exist in the population (Rice et al. 1993b). Interestingly, despite evidence of more size-selective mortality in the high-variance treatments, which should lead to larger survivors (Folkvord and Ottera 1993; Rice et al. 1993b; Hopper et al. 1996), final mean sizes did not differ between the two treatments.

The results of my experiments, which indicate an interaction between initial variation and selective mortality, have a number of population level consequences. First, since survival can be influenced by initial variability in a characteristic such as size, the number of YOY fish recruited into a population could be affected by this initial variation. In addition, the type of mortality that operates on a cohort could be a function of initial size variation, with selective mortality less likely when variation is low. One situation that can establish large variation in size quickly is density-dependent growth; increased competition in high densities can lead to unequal food partitioning (Rubenstein 1981; Lomnicki 1988). In fact, in a related pond experiment, YOY populations that were initially at very high densities did exhibit more intense size-selective mortality, as well as higher overall mortality, than YOY populations from lower initial densities; the survivors from the former also had tighter final size-distributions (Chapter 2).

As selective mortality tends to tighten size distributions, a further consequence would be that the final survivors will be more uniform, at least with respect to size (Hopper et al. 1996). For fathead minnows, the next major source of mortality following the first growing season is overwinter mortality, and this mortality is also size-dependent

(Post and Evans 1989, Johnson and Evans 1996); thus, if selective mortality during that first growing season is significant, the amount of initial variation in size may ultimately have consequences as to who, and how many, cohort members survive the winter. During a mild winter, a cohort with little variability in size would probably do well, but it may be that only the very largest fish can survive a severe winter, in which case a cohort with little size-variability could do poorly, as it would have very few fish above the threshold size required for survival.

To date, consequences of the amount of variation in characteristics among individuals, in terms of the number and characteristics of survivors, have been studied in simplified laboratory experiments or in simulation models. My experiment was in a more natural setting, and at larger spatial and temporal scales than previous studies, yet my results suggest that the relationships found in earlier studies have generality. Not all the earlier predictions held; in particular, the final average size of survivors was not related to initial size variation, perhaps due to an interaction between behaviour, growth, and vulnerability to predation. Because such interactions are more often seen in natural settings than in the simplicity of the laboratory, it is important that we incorporate these complexities into our population-level tests, if we wish to impart realism into our understanding of processes controlling recruitment.

Table 3-1: Maximum sizes (total length) of young-of-the-year (YOY) fathead minnow prey either consumed by various size-classes of older (≥ age-1) fatheads or attacked and killed but not fully consumed.

Adult Size Class (mm)	*Largest YOY Eaten Whole (mm)*	*Largest YOY Attacked and Killed (mm)*
50-54	11	13
55-59	13	15
60-64	13	15
65-69	17	19
70+	19	21

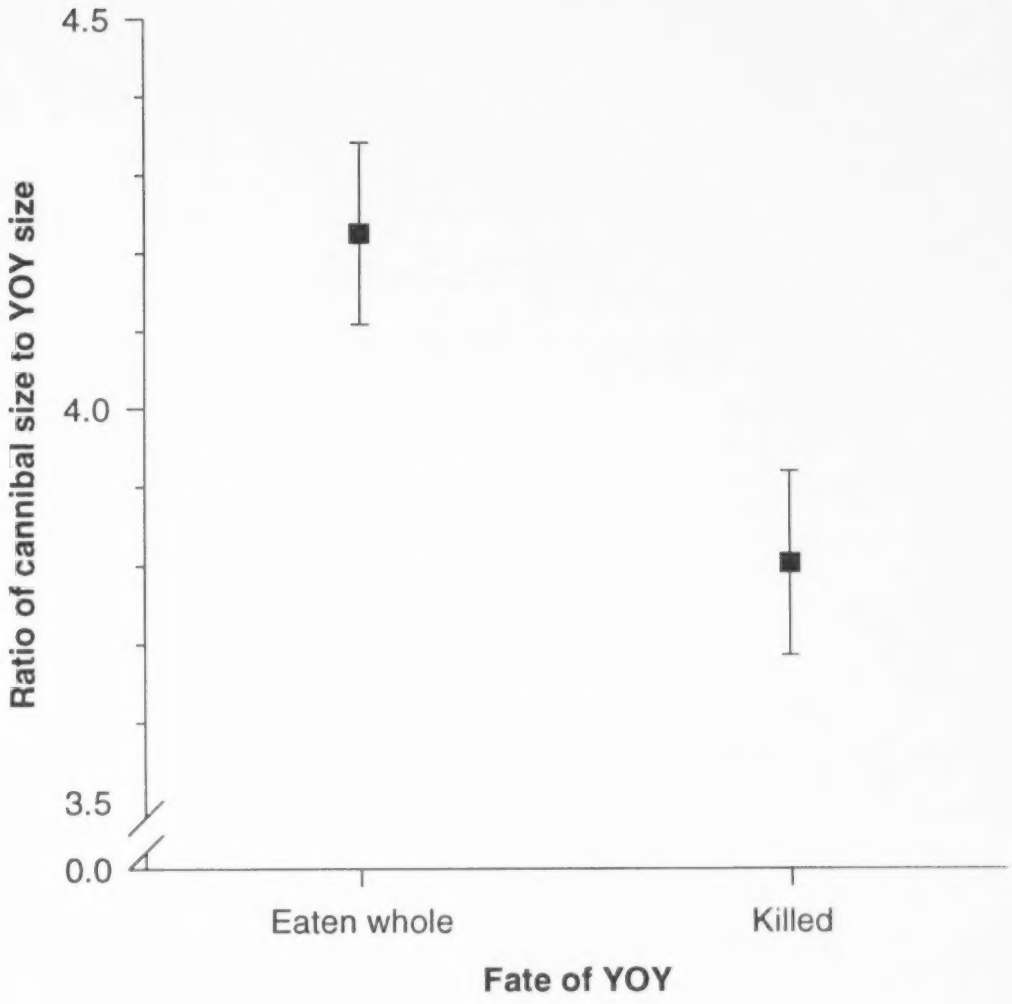

FIG. 3-1. The average ratio (± SE) of adult size to maximum size of YOY that adults were able to eat whole or kill but not consume in laboratory experiments on cannibalism.

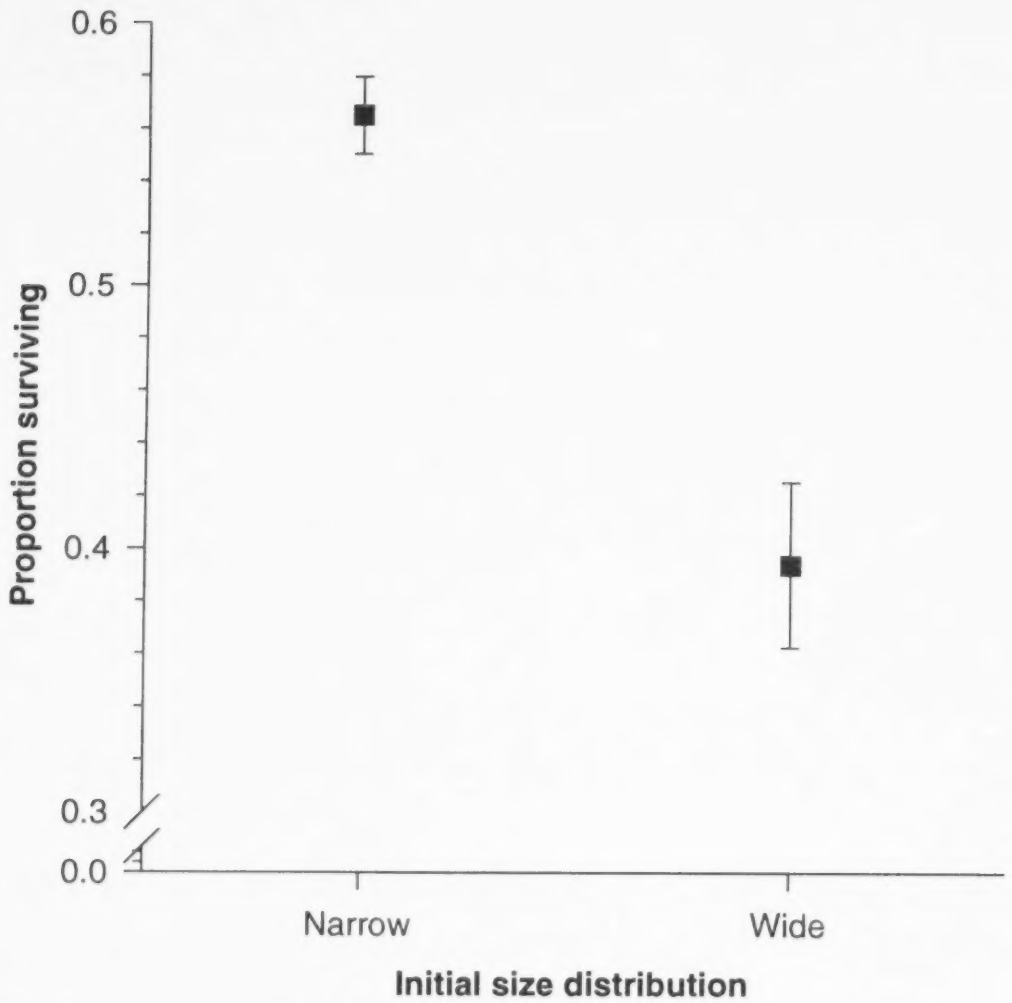

FIG. 3-2. Survival (± SE) of YOY fathead minnows in the two size-variation treatments of the pond enclosure experiment.

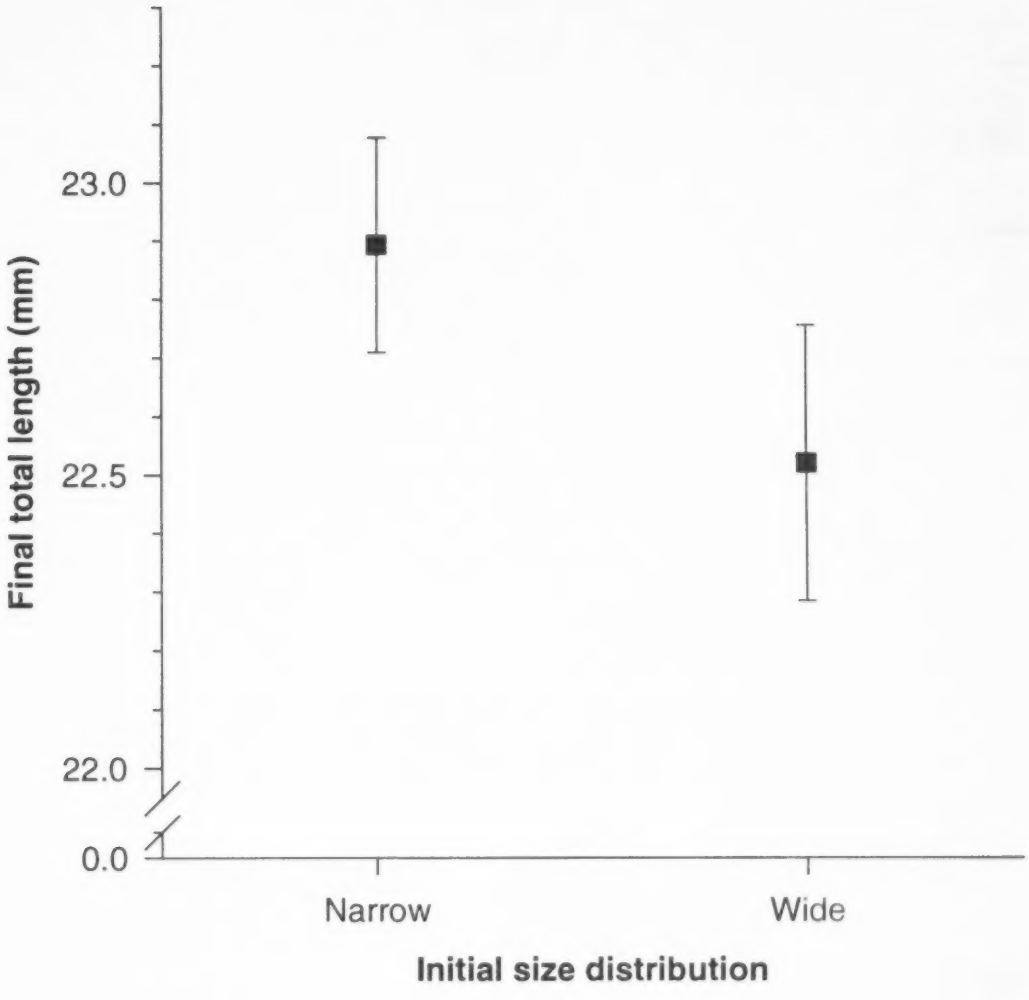

FIG. 3-3. Final total lengths (± SE) of the surviving YOY fathead minnows from the two size-variation treatments.

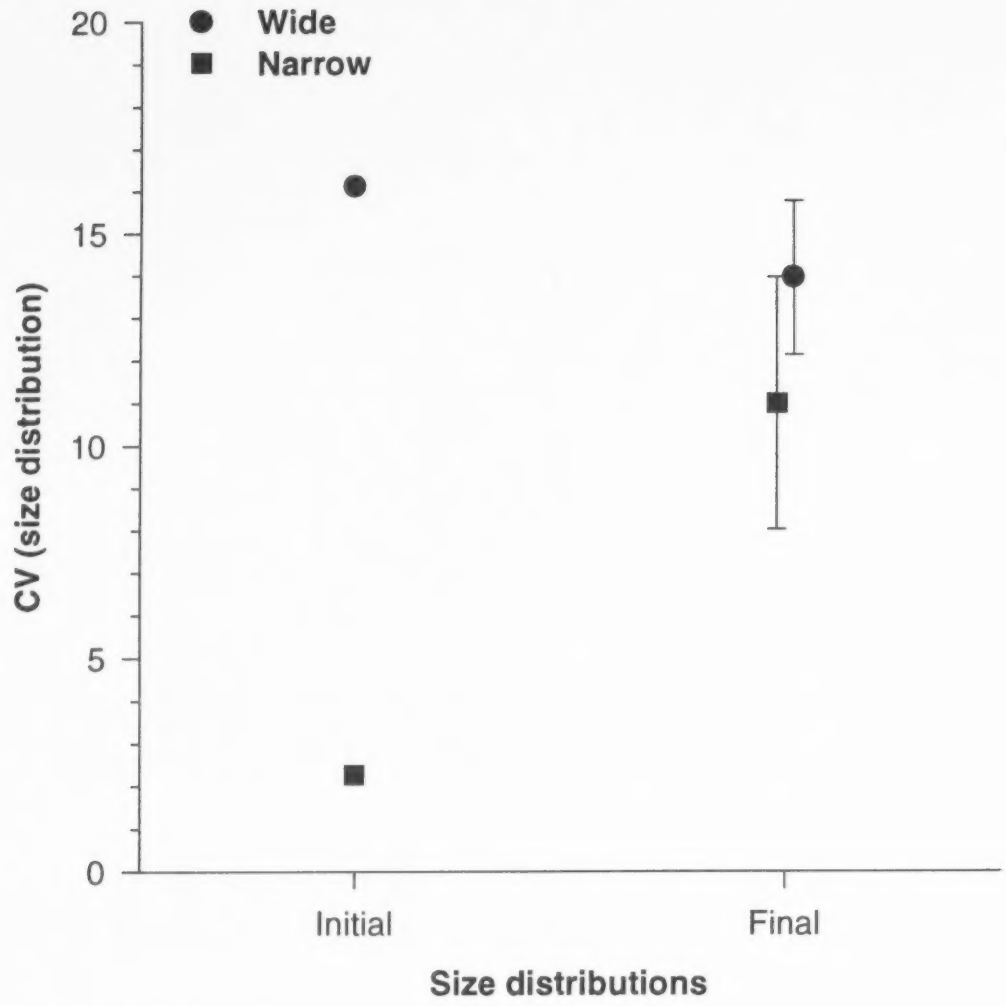

FIG. 3-4. A comparison of the coefficient of variation (CV) of the YOY size distributions (± SE) at the beginning and end of the experiment on the consequences of size-variation.

LITERATURE CITED

Arcese, P., J. N. M. Smith, W. M. Hochachka, C. M. Rogers, and D. Ludwig. 1992. Stability, regulation, and the determination of abundance in an insular song sparrow population. Ecology 73: 805-822.

DeAngelis, D. L., and L. J. Gross. 1992. Individual-based models and approaches in ecology. Chapman & Hall, New York, New York, USA.

Dong, Q., and G. A. Polis. 1992. The dynamics of cannibalistic populations: a foraging perspective. Pages 13-37 *in* M. A. Elgar and B. J. Crespi, editors. Cannibalism: ecology and evolution among diverse taxa. Oxford University Press, New York, New York, USA.

Elliot, J. M. 1989. Mechanisms responsible for population regulation in young migratory trout, *Salmo trutta*. I. The critical time for survival. Journal of Animal Ecology 58: 987-1001.

Ellis, S. C., W. O. Watanabe, and W. D. Head. 1993. Effect of initial age variation on production of Florida red tilapia fry under intensive, brackishwater tank culture. Aquaculture and Fisheries Management 24: 465-471.

Folkvord, A., and H. Ottera. 1993. Effects of initial size distribution, day length, and feeding frequency on growth,survival, and cannibalism in juvenile Atlantic cod (*Gadus morhua* L.). Aquaculture 114: 243-260.

Harris, R. N. 1987. An experimental study of population regulation in the salamander, *Notophthalmus viridescens* dorsalis (Urodela: Salamandridae). Oecologia 71: 280-285.

Held, J. W., and J. J. Peterka. 1974. Age, growth and food habits of the fathead minnow, *Pimephales promelas*, in North Dakota saline lakes. Transactions of the American Fisheries Association 4: 743-755.

Hopper, K. R., P. H. Crowley, and D. Kielman. 1996. Density dependence, hatching synchrony, and within-cohort cannibalism in young dragonfly larvae. Ecology 77: 191-200.

Huston, M. A., and D. L. DeAngelis. 1988. Size bimodality in monospecific populations: a critical review of potential mechanisms. The American Naturalist 129: 678-707.

Huston, M. A., D. L. DeAngelis, and W. M. Post. 1988. New computer models unify ecological theory. BioScience 38: 682-691.

Johnson, T. B., and D. O. Evans. 1996. Temperature constraints on overwinter survival of age-0 white perch. Transactions of the American Fisheries Society 125: 466-471.

Litvak, M. K., and W. C. Leggett. 1992. Age and size-selective predation on larval fishes: the bigger-is-better hypothesis revisited. Marine Ecology Progress Series 81: 13-24.

Lomnicki, A. 1988. Population ecology of individuals. Princeton University Press, Princeton, New Jersey, USA.

Maret, T. J., and J. P. Collins. 1994. Individual responses to population size-structure: the role of size variation in controlling expression of a trophic polyphenism. Oecologia 100: 279-285.

-------. 1996. Effect of prey vulnerability on population size-structure of a gape-limited predator. Ecology 77: 320-324.

Margulies, D. 1990. Vulnerability of larval white perch, *Morone americana*, to fish predation. Environmental Biology of Fishes 27: 187-200.

Miller, T. J., L. B. Crowder, J. A. Rice, and E. A. Marschall. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. Canadian Journal of Fisheries and Aquatic Sciences 45: 1657-1670.

O'Neill, K. M. 1992. Body size asymmetries in predatory interactions among robber flies (Diptera: Asilidae). Annals of the Entomological Society of America 85: 35-38.

Post, J. R., and D. O. Evans. 1989. Size-dependent overwinter mortality of young-of-the-year yellow perch (*Perca flavescens*): laboratory, in situ enclosure, and field experiments. Canadian Journal of Fisheries and Aquatic Sciences 46: 1958-1968

Post, J. R., and A. B. Prankevicius. 1987. Size-selective mortality in young-of-the-year yellow perch (*Perca flavescens*): evidence from otolith microstructure. Canadian Journal of Fisheries and Aquatic Sciences 44: 1840-1847.

Price, C. J., W. M. Tonn, and C. A. Paszkowski. 1991. Intraspecific patterns of resource use by fathead minnows in a small boreal lake. Canadian Journal of Zoology 69: 2109-2115.

Rice, J. A., L. B. Crowder, and M. E. Holey. 1987. Exploration of mechanisms regulating larval survival in Lake Michigan bloater: a recruitment analysis based on characteristics of individual larvae. Transactions of the American Fisheries Society 116: 703-718.

Rice, J. A., L. B. Crowder, and K. A. Rose. 1993a. Interactions between size-structured predator and prey populations: experimental test and model comparison. Transactions of the American Fisheries Association 122: 481-491.

--------, T. J. Miller, K. A. Rose, L. B. Crowder, E. A. Marschall, A. S. Trebitz, and D. L. DeAngelis. 1993b. Growth rate variation and larval survival: inferences from an individual-based size dependent predation model. Canadian Journal of Fisheries and Aquatic Sciences 50: 133-142.

Robinson, C. K., and W. M. Tonn. 1989. Influence of environmental factors and piscivory in structuring fish assemblages of small Alberta lakes. Canadian Journal of Fisheries and Aquatic Sciences 46: 81-89.

Rubenstein, D. I. 1981. Individual variation and competition in the Everglades pygmy sunfish. Journal of Animal Ecology 50: 337-350.

Scott, W. B. and E. J. Crossman. 1973. Freshwater Fishes of Canada. Department of Fisheries and Oceans, Ottawa, Ontario, Canada.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry: Second Edition. W.H. Freeman and Co. San Francisco, California, USA.

Unger, L. M. 1983. Nest defense by deceit in the fathead minnow, *Pimephales promelas*. Behavioral Ecology and Sociobiology 13: 125-130.

VanBuskirk, J. 1989. Density-dependent cannibalism in larval dragonflies. Ecology 70: 1442-1449.

VanWinkle, W., K. A. Rose, and R. C. Chambers. 1993. Individual-based approach to fish population dynamics: an overview. Transactions of the American Fisheries Association 122: 397-403.

Wilkinson, L. 1992. SYSTAT: the System for Statistics. Systat Inc., Evanston, Illinois, USA.

CHAPTER 4

GENERAL DISCUSSION AND CONCLUSIONS

Understanding how animal populations are regulated in natural systems remains one of the most fundamental questions in ecology. There is now general consensus that regulation occurs through density-dependent processes (Sinclair 1989; Turchin 1995), yet for species with stage-structured life-histories, we know little about the how these mechanisms act and interact among stages. Mechanisms acting among individuals within one life-history stage may also play an important role in recruitment; differences among individuals with respect to characteristics such as size, hatch date, age, or growth rate may influence how many, and which, individuals in a cohort survive (Huston et al. 1988). We do not yet understand how differences in the variability of these characteristics within a cohort may affect recruitment at the population level.

In this thesis, I demonstrate experimentally that density-dependent processes acting on and between adult, egg, and YOY stages have potential to strongly regulate recruitment in populations of fathead minnows under field conditions. Density-dependent mechanisms acting within and among the life-stages present in the first growing season affected not only the abundance of survivors at the end of the season, but were important in determining the characteristics of the surviving YOY fish (Chapter 2). In particular, the variability in size among the survivors was affected by the action and interactions of these processes, and there was indication that this variability can translate into population-level consequences, affecting how many, and which individuals survive through the first winter. There is even some indication that variation in mid-season sizes of YOY may be

related to initial post-hatch density of the cohort. In a related experiment, I demonstrated that such mid-season size variation among YOY cohorts, in turn, has strong affects on end-of-season survival (Chapter 3). And, likely because vulnerability to cannibalism by older life-stages is size-related, this variability in size also affected the intensity of size-selective mortality. As in the previous experiment, the characteristics displayed by individuals at the end of the first growing season were dependent on how intensive that selection was.

Many recent theoretical studies contend that explicitly considering differences among individuals is vital to fully understand population dynamics (Huston et al. 1988; DeAngelis and Gross 1992; VanWinkle et al. 1993); results from my enclosure study give empirical support to this contention. Differences in the amount of variability in individual characteristics that I observed, which already had population-level consequences by the end of the first growing season, would also suggest that the differences in variability at the end of the season can have strong effects on survival through the winter and ultimately on recruitment into the adult population. Studies on processes occurring during the first growing season would also benefit from the added resolution that otolith analysis techniques add; growth rates and sizes of YOY fish at different times during the first year may be back-calculated using daily rings on the otoliths (Campana and Neilson 1986), but this technique must be validated separately for each and every fish species used.

One fundamental goal of population ecology is to be able to predict dynamics of populations in natural situations. Recently, studies on fish populations have tended to concentrate on processes occurring in only one or two life stages. Yet my study

demonstrates that the regulation of recruitment in fish populations is not a simple matter of processes occurring in just one or two stages; mechanisms acting during each life stage are connected, via a series of cascading life-history interactions, and as a unit are important in determining how many, and which individuals survive. These processes and their interactions are simple enough to be incorporated into a predictive model on fathead minnow population dynamics, but my study suggests that to achieve general understanding of fish population dynamics we need to understand where, how strong and how frequently these processes occur in a range of species. In conclusion, my investigation has shown that future predictive studies of fish population dynamics must consider processes occurring at all life stages, and that dynamics occurring during the YOY stage should be represented at the individual level.

LITERATURE CITED

Campana, S. E., and J. D. Nielson. 1985. Microstructure of fish otoliths. Canadian Journal of Fisheries and Aquatic Sciences 42:1014-1032.

DeAngelis, D. L., and L. J. Gross. 1992. Individual-based models and approaches in ecology. Chapman & Hall, New York, New York, USA.

Huston, M. A., D. L. DeAngelis, and W. M. Post. 1988. New computer models unify ecological theory. BioScience 38:682-691.

Sinclair, A. R. E. 1989. Population regulation in animals. Pages 197-241 *in* J. M. Cherrett, editor. Ecological concepts. Blackwell Scientific, Oxford, UK.

Turchin, P. 1995. Population regulation: old arguments and a new synthesis. Pages 19-37 *in* N. Cappuccino and P. W. Price, editors. Population dynamics: new approaches and synthesis. Academic Press Inc., New York, New York, USA.

VanWinkle, W., K. A. Rose, and R. C. Chambers. 1993. Individual-based approach to fish population dynamics: an overview. Transactions of the American Fisheries Society 122: 397-403.